Exploring the potential impacts of global change on the woody component of South African savannas

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Abstract

Land cover change, elevated CO_2 and associated climate change are driving changes in ecosystem structure and function across the world. These changes are best described and understood in northern hemisphere temperate systems. Studies, models and reports from these regions are therefore often used as the basis for understanding, predicting and managing change in other biomes, including African savannas. In savannas elevated CO_2 has been implicated in driving an increase in woody cover, however attribution to global drivers is often confounded by land-use management which is also implicated as a driver of tree cover increases. Climate change is predicted to directly drive species range shifts in savannas, however several important gaps exist in the literature which prevent the development of a clear predictive framework to describe these changes. Whilst climate is often assumed to be the primary factor underlying savanna tree distribution this has not been demonstrated for savanna tree species. Additionally the determinants of individual savanna species distributions have seldom been investigated. The few existing studies are correlative species distribution models based on adult plant distribution and underlain by the assumption that climate sets plant distribution. Although a demographic approach is very important in understanding tree: grass coexistence in savannas, this approach is seldom used in understanding species distributions.

The aim of this study was therefore to assess how global change might influence South African savannas. We place emphasis on the role of elevated CO_2 and climate change. I first report on an analysis of historical changes in woody plant abundance at large spatial scales to assess the magnitude of tree cover change in South African savannas. I attempt to untangle the role of local drivers and global drivers in causing tree cover changes from 1940 - 2009. I then report on studies aimed at determining what limits the distribution range of two common savanna trees *Acacia nigrescens* and *Colophospermum mopane,* at three critical demographic stages. Here I used a series of field studies, transplant experiments, lab experiments and modelling to determine the critical drivers of the distribution of these plants so as to understand how savanna plants might respond to changing climates.

Using a natural experiment of four different land-use systems across the savanna rainfall gradient, I measured the magnitude and trajectory of tree cover change from the aerial photographic records from 1940 to 2009. I used this natural experiment, to untangle the role of local vs. global drivers. Each land use should have different trajectories of tree cover

change, unless a global driver is causing the increases. Tree cover increased across all land uses across the rainfall gradient, except in the presence of elephants in the low rainfall areas. The results suggest that elevated CO_2 is driving an increase in tree cover across South African savannas

To understand savanna tree species response to climate change I investigated the drivers of their distribution limits. I first used a traditional species distribution climate based approach to generate hypotheses as to which regional-scale climatic drivers might determine the distribution of *C. mopane*. Temperature, rainfall and latitude were the most important predictors of *C. mopane* range limits, and were therefore considered in subsequent chapters where I examined the drivers of distribution limits at each demographic stage.

At the germination and early seedling establishment phases of *C. mopane* and *A. nigrescens*, I used a lab experiment and a soil water model parameterized with measurements from the lab study to examine if temperature and water stress interact to limit either germination or seedling establishment of *C. mopane.* Germination events were not limited but seedling establishment events were limited by water availability. The study suggests that warmer future conditions will accelerate the rate of radicle extension and increase the frequency of seedling establishment events.

At the sapling stage I established a transplant experiment where *C. mopane* and *A. nigrescens* were planted at four paired, high and low elevation sites across an 850 km latitudinal gradient. This seems to be the first attempt to experimentally explore the climatic limits of African savanna tree distribution by determining tree survival and growth at latitudes and altitudes much broader than the distribution limits of the study species. Neither climate nor presence within a distribution range could explain plant performance. Grass competition significantly affected plant growth rates, but alone could not explain the distribution limit. Species distributions were best predicted when maximum tree growth rates in the presence of grass were considered in relation to local fire return intervals. The probability of sapling escape from the fire trap was the most likely determinant of distribution limits of these two species.

At the adult stage I examined the ecophysiology of adult *C. mopane* using a watering experiment to explore the role of water and temperature in controlling photosynthesis and leaf phenology. Water was a proximate cue in driving leaf loss of *C. mopane*. Leaf carbon acquisition rates do not decline through leaf aging, but are strongly affected by soil moisture

availability and temperature. Although the physiology and phenology of this plant is driven by water and temperature we did not demonstrate, within reasonable climatic limits, any limitations upon this adult stage.

Elevated CO_2 appears to be driving a large scale regional increase in tree cover across South African savannas with local modification by land use. My studies to identify drivers of the distribution limits of *C. mopane* and, to a lesser extent, *A. nigrescens* demonstrated that the determinants of ranges in these tropical savanna species are complex, and multiple factors interact to affect the performance and success of these species at different demographic stages. Critical range limitation is most likely to occur at the sapling stage where a combination of higher grass biomass and frequent fire return intervals are important in determining the escape of these trees from the fire trap.

This thesis offers new insights into how savanna species will respond to two critical changes. Tree cover increases and, potentially, associated biome shifts are likely. The lack of any clear direct climate limitation on the study species indicates that range shifts are unlikely to occur in response to altered climates. Consumer controls e.g. by fire are important determinants of the distribution of savanna species. Future research should focus not only on global change impacts on plant growth, but also in how climate change will impact consumer controls. The combination of the findings in this thesis makes a novel contribution to science and savanna ecology by providing a new framework from which to consider global change in savannas.

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General Introduction

Global change, driven by exponential increases in the human population, land cover change, elevated CO_2 and its associated effects on climate change, is transforming the planet (Vitousek, 1994). The global ecological and economic impact of these changes has received much attention (Millennium Ecosystem Assessment, 2005; IPCC, 2013), however these reports are dominated by case-studies and data largely collected from northern hemisphere temperate systems (Thomas, 2010; IPCC, 2013). Regional changes and their associated ecosystem responses have been under-investigated in the southern hemisphere, particularly within the savanna biome. Given the importance of this biome, an improved understanding of the magnitude of changes and how ecosystems and species are going to respond is needed. Savannas are one of the world's largest biomes (Scholes & Archer, 1997) covering approximately 20% of the earth's surface, and contributing ~30% of terrestrial net primary production (NPP) (Lloyd et al. 2008; equal to that of tropical forests). Between 40 and 65% of the African continent is covered by savanna (Huntley & Walker, 1982; Scholes & Walker, 1993) where it is home to one fifth of the global human population and a majority of its rangelands and livestock (Scholes & Archer, 1997). Savannas are also home to a large proportion of the world's extant large mammals, especially megaherbivores (Owen-Smith, 1988).

Determinants of savanna structure and function

Distribution of the African savannas

To understand potential global change impacts on savannas, the underlying drivers of savanna structure and function must be clarified. The distribution of the biomes of the world is often assumed to be controlled by climate so that, for example, their location can be predicted from precipitation and temperature (Whittaker, 1975). When mapped according to Whittaker's precipitation: temperature relationship, for example, the savanna climate space is occupied by three structurally and functionally different biomes; savanna, grassland and forest (Whittaker, 1975). Scholes & Walker (1993) suggest an alternative climate classification for savannas where their distribution can be predicted by a mean monthly temperature of > 10°C, high rainfall seasonality with sufficient moisture for 60 days of plant growth, and a wet warm season followed by a cooler dry season. This system still defines a

climate space where forests and thickets are interspersed within the savanna (Russell-Smith et al, 2004; Lehmann, 2011; Parr et al, 2012). Savannas are therefore amongst the most extensive vegetation area not at equilibrium with climate (Bond & Keeley, 2005a; Bond et al, 2005b, Pausas & Keeley, 2008; Bowman et al, 2009; Hirota et al, 2011; Lehmann et al, 2011; Staver et al, 2011). Instead most savannas are consumer controlled systems, where fire and herbivory act upon the vegetation structure and composition to keep it below its climatic potential (Bond et al, 2005c). Lehmann et al. (2011) determined that the distribution of African savannas is defined by interactions between climate, disturbance and vegetation which promotes woody growth and influences fire regimes. The mesic limits of African savannas appear to be limited by fire and the climatic and vegetation properties that influence the fire regime (Archibald et al, 2009; Staver et al, 2011). Determinants of the limits of arid savannas are less clear, they occur when there is low annual rainfall (~200mm), high rainfall seasonality or high soil fertility, a factor which suggests that herbivores, especially in the more fertile areas, can extend the limits of savanna (Lehmann et al, 2011). Certainly herbivores have a higher density in the drier areas coupled with a disproportionately large effect on reducing woody plant growth in drier systems, presumably due to lower compensatory growth of plants after losses to herbivores (Pringle et al, 2007; Asner et al, 2009.)

Shifting controls on savanna function across environmental gradients

As climate, vegetation and disturbance interact to determine the distribution of savannas, how is this interaction expressed within a savanna? Savannas can be divided into climatically determined, stable savannas and disturbance controlled unstable savannas (Figure 1d) (Sankaran et al, 2005). Stable savannas occur where rainfall is < ~ 650 - 780mm. Here water availability is the primary constraint on maximum tree cover (Sankaran et al, 2005; Archibald et al, 2009). Although fire, herbivory and soil characteristics may interact to reduce tree cover below maximum levels, the upper limit of tree cover is defined by water availability. Fires seldom burn areas with an annual rainfall of < 300mm, since grass fuel is insufficient in most years to support a fire (Trollope et al, 2002). Above this lower limit, the percentage burnt area increases near linearly with rainfall (Figure 1c) (Lehmann et al, 2011), as does grass biomass (Deshmukh et al 1984; O'Connor et al, 2001) (Figure 1b). Tree grass interactions are primarily facilitative (Figure 1a) (Dohn et al, 20xx), and herbivore biomass (both grazers and browsers) also increases with rainfall (Figure 1c). Coe et al. (1976) describe the herbivore: rainfall relationship as curvilinear with an inflection point between 800-900mm. Using the

equation from Fritz & Duncan (1994), herbivore biomass increases linearly to a slightly lower inflection point at around ~750mm (Hempson et al, *unpublished data*; Fritz & Duncan, 1994). Herbivore biomass probably peaks at a rainfall threshold between 750-850mm, near the divide between stable and unstable savannas. Wet season droughts are common, especially at the more arid end, and the critical tree establishment bottleneck is most likely to occur during the seedling establishment phase (Higgins et al, 2000). After germination, there is a critical window for seedling establishment (Botha, 2006) when seedlings need to extend their radicles out of the evaporation zone in the surface soil layers to the more stable moister sub-soil layers (Higgins et al, 2000, Wiegand et al, 2006, Bond, 2008). The success of the seedling is dependent on sufficiently frequent rains to keep surface soil layers moist for ~ 1 month, during this window period.

Mesic (unstable) savannas, where rainfall exceeds ~650 -750mm are consumer controlled systems as the vegetation is not at equilibrium with the climate (Sankaran et al, 2005; Staver et al, 2011) (Figure 1d). Here tree cover does not increase linearly with rainfall as there is sufficient available moisture for rainfall not to limit tree growth. Tree canopy closure is possible and disturbances in the form of herbivory and fire are essential to maintain tree: grass co-existence, and hence savannas. Regional scale studies of grass biomass across the rainfall gradient indicate that grass biomass increases linearly with rainfall, but these studies seldom include sites with >1020mm (Deshmukh, 1984; O'Connor et al, 2001). O'Connor et al (2001) present a graph of grass biomass against rainfall and, although this is presented as a linear relationship, the points at 1020mm are lower than the suggested relationship (Figure 1b). In these mesic savannas, the relationship between trees and grasses switches from facilitative to competitive (Dohn et al, 2013) (Figure 1a). Fire frequencies are high (Figure 1c) which can prevent trees from establishing. If tree cover exceeds a threshold of ~40% grass fuel production declines and fire is excluded from the area (Scholes, 2003; Riginos, 2009, Archibald et al, 2009), potentially initiating a switch to an alternative state (forest) (Staver et al, 2011). High fire frequencies, coupled with browsing pressure may impose a critical demographic bottleneck on tree establishment at the sapling stage. Saplings growing in the presence of grass are vulnerable to fire-induced top-kill, knocking the saplings back, essentially trapping them in the grass layer (Frost, 1984; Higgins et al, 2000; Bond, 2008, Williams, 2009; Prior et al, 2010; Werner & Franklin, 2011). As these plants are often very tolerant to fire they experience low mortality, instead resprouting in response to topkill (Cesar & Menaut, 1974; Sarmiento, 1985; Higgins et al, 2000; Bond, 2008; Hoffman et al, 2009;

Williams, 2009). Plants escape from the fire trap when they have reached a threshold size (often ~3m in height or a minimum threshold stem diameter) where the canopy is out of the topkill zone (Bond, 2008).

Thus the relative importance of soil moisture, herbivory, and fire in structuring savannas changes across the environmental gradient of savannas, and the plants within each gradient have traits related to tolerating/persisting in the presence of the dominant drivers (Staver et al, 2012). Seedling recruitment limitation should occur at low rainfall sites, and sapling release limitation of adult trees at high rainfall. Fire tolerant plants occurring in areas of frequent fire may have fire adapted traits such as pole-like sapling architecture, rapid growth rates and below ground storage reserves to facilitate rapid growth following a burn (Frost, 1984; Sarmiento et al, 1985; Gignoux et al, 1997; Archibald & Bond, 2003; Hoffman et al, 2003a; Schutz et al, 2009; Staver et al, 2012). Herbivory tolerant plants which are prevented from recruiting to adults due to heavy browsing pressures may develop a cage-like architecture, often associated with thorns, to minimise above ground biomass loss to herbivory (Archibald & Bond, 2003; Bond 2008; Staver et al, 2012). While this conceptual framework allows many predictions to be made, a gap in knowledge is an understanding of the importance of rainfall driven germination and seedling establishment across the rainfall gradient.

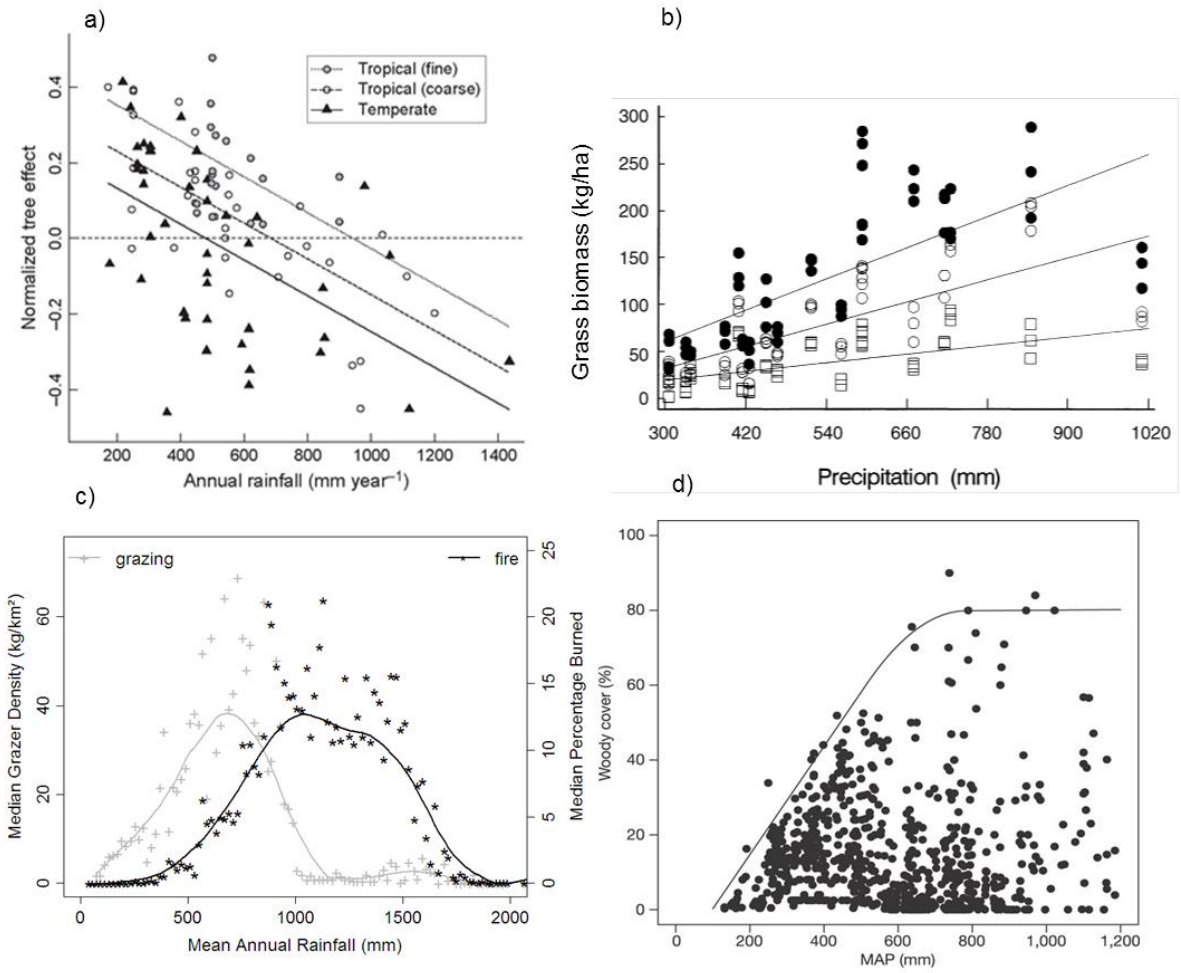

Figure 1: Key savanna processes that change across the rainfall gradient. Figures are all from African savannas. a) Tree grass interactions are facilitative at low rainfall but as rainfall increases interactions become increasingly competitive (Figure from Dohn et al, 2013), b) Grass biomass increases linearly across the rainfall gradient (Figure from O'Connor et al, 2001) c) Change in burnt area across the rainfall gradient (Figure from Lehman et al, 2011) and herbivore density across the rainfall gradient (Unpublished data based on Fritz and Duncan, 1994 and FAO grazer densities in Archibald et al, 2009) d) Changes in maximum tree cover across the rainfall gradient (Figure from Sankaran et al, 2005).

Land use and land management in savannas

African savannas have had a long history of utilization by humans, and some of the world's oldest hominid fossils have been discovered in this biome (Bell, 1971; Scholes & Walker, 1993). However following an increase in human population over the last century, an increase in land transformation, cultivation and land-use intensity has occurred in savannas (Millennium Ecosystem Assessment, 2005; Coetzer et al, 2010). Over the last century fencing, coupled with land-use intensification, has created a fragmented savanna landscape

with multiple management systems. At present, savanna land-use in South Africa can be divided into three dominant management systems; communally owned subsistence farming, commodity or commercial farming and conservation (Scholes & Walker, 2003, Scholes, 2009).

In a South African context communal rangelands are former 'homelands' established as self governing territories created through forced resettlement of 3.5 million people during the apartheid era (Shackleton et al, 2001, Wessels et al, 2013). Here rural communities rely on a variety of natural resources and ecosystem services for their own consumption or sale (Cousins, 1999; Shackleton & Shackleton, 2000, Shackleton, 2007). Most rural households (70 – 100%) are reliant on indigenous wood for fuel, building or sale, but the heavy wood extraction rates are considered unsustainable (Banks et al, 1996, Matsika et al, 2012; Wessels et al, 2013). Most rural households use the land as a source of wild fruits, herbs and medicinal plants (Shackleton et al, 2001). Approximately 30% of households rely on the land for livestock grazing. Livestock are kept for multiple purposes e.g. slaughter, sale, draught power, and as a store of wealth- which is particularly true for cattle (Cousins, 1999; Higgins et al, 1999). The aim of communal farmers is generally accepted as being to maximise animal numbers (Vetter, 2003). The areas are unfenced and communally used.

Commercial farming in savannas is primarily concerned with livestock production. The management model is based on land users' aims to maximise saleable off take from the herd. Stocking rates are often based on growth curves to maximise meat yield (Vetter, 2003). The result is a grazer dominated system with moderate but relatively constant stocking rates. Frequently farmers apply a policy of fire suppression (Higgins et al, 1999).

In the past two decades, many commercial cattle ranches in South Africa have changed from commercial farming to private conservation land use. In these areas, the primary management objectives are geared towards hunting, game sales and eco-tourism (Sims-Castley et al, 2005). Here, management actions often aim to maintain high densities of wild herbivores to improve the hunting/sales/tourism experience, achieved by the wide-scale provision of artificial water points, salt-licks or even fodder in times of high stress or low primary production (Walker et al, 1987). These actions can change herbivore distribution patterns and densities (Smit et al, 2007, Loarie et al, 2009) and cause corresponding changes in the vegetation (Parker & Witkowski, 1999, Brits et al 2002). State-run conservation concerns are essentially the reference state of savannas as a full complement of fire and herbivory

processes have been maintained (Scholes, 2009). Management aims are to maximize biodiversity (e.g. Du Toit et al, 2003)

Change in savannas

The above framework of savanna structure and function provides context from which to understand local and global change in savannas, natural or otherwise. The Millennium Ecosystem Assessment (2005) identifies habitat change and over-exploitation as the largest threats to savanna system integrity. These threaten to accelerate land degradation, which broadly describes the loss of natural capital and system productivity (UNCCD, 1994). The symptoms of functional shifts include changes in plant species composition, changes in the dominant functional types, and changes in vegetation structure in the form of bush encroachment, range shifts and alien species invasion, change in the grass sward species composition and a reduction in cover (Scholes, 2009). Other characteristics are reduced soil infiltration and soil erosion. Historically these syndromes of land degradation were considered to be driven by local land use where over-grazing, over harvesting and in some cases by under grazing and were often raised as local scale issues of concern (Archer et al, 1995; Roques et al, 2000; Fynn & O' Connor, 2000; Hoffmann & Ashwell, 2001; Fensham et al, 2005). Although this threat still remains, potentially larger scale factors also pose a pressing risk to savanna structure, composition and function and need to be considered.

Regional scale manipulation of fire and herbivory

A mosaic of management approaches against a backdrop of an exponentially increasing human population has caused an alteration in two fundamental processes governing savanna dynamics; fire and herbivory. Africa is remarkable in retaining areas where large populations of native ungulates and megaherbivores exist in contrast to most parts of the world where megafaunal extinctions followed human settlement (Owen-Smith, 1988; Johnson 2009). Although humans in savannas have a long history (Harris, 1980; Scholes & Walker, 1992), the past ~120 years expanding human settlements, heavy hunting and ivory and rhino horn exploitation has lead to wide scale reductions in wild ungulate and megaherbivore numbers. Free-roaming large herbivores have disappeared from large parts of Africa and are increasingly replaced by livestock (predominately cattle) (Augustine & McNaughton, 1996; Lamprey and Reid 2004), or they are confined to fenced conservation areas (Owen-Smith, 1988). This regional change has caused a switch towards grazer dominated systems. Waterhole provision and fencing has lead to more concentrated sedentary herbivore

populations and the general loss of migratory systems (Walker et al, 1987; Augustine & McNaughton, 1998; Smit et al, 2007; Fynn & Bonyongo, 2011). These changes have the potential to alter vegetation structure and community composition.

Mammalian herbivores whilst depending on plant communities also exert strong effects on plants and their wider communities (Bell, 1971; Cumming, 1982, Dublin et al, 1990). Herbivores and herbivory affect ecosystem processes such as nutrient cycling (Hobbs, 1996; McNaughton et al, 1997; Frank et al, 2000, Pringle et al, 2007; Anderson et al, 2007), disturbance regimes and, through this, the tree: grass balance. Grazing and large herbivore trampling can reduce fire return intervals (Hobbs, 1996; Holdo et al, 2009, Archibald et al, 2009; Asner et al, 2009), which can increase woody vegetation cover by reducing fire frequencies and grass root competition (Van Vegten, 1984; Roques et al, 2001). Browsers can change the properties of the dominant plant species and alter plant growth rate and nutrient uptake (Augustine & McNaughton, 1998). Heavy browsing can alter the species composition of an area, either through increasing the dominance of browse tolerant species or through the loss of browse intolerant plants (Augustine &McNaughton, 1998; Wigley et al, 2014). Browsing can reduce tree cover (Levick et al, 2009) and affect the structure of plants, often preventing vertical growth (Cumming, 1982; Augustine & McNaughton, 1998; Levick et al, 2009; Holdo et al, 2009; Moncrieff et al. 2013). This action can cause demographic limitations on trees (Higgins et al, 2000; Staver et al, 2009; Midgley et al, 2010), often keeping plants trapped in the browse trap, thus keeping plants exposed to browsers and fire (Dublin et al, 1990; Higgins et al, 2000; Staver & Bond 2014).

The mosaic of management has not only altered mammal assemblages but also caused large shifts from the "natural" fire regime. Besides direct suppression of fires, we have altered fire regimes by changing fuel continuity as a result of high road densities, human settlements, grazing and the presence of transformed land all resulting in a reduction of the amount of area burnt within savannas (Archibald et al, 2009). The area burnt by fire will therefore likely be lower in communal and conservation areas than the past. The presence or absence of fire or alteration of fire frequencies can affect ecosystem characteristics. Fire exclusion, especially in mesic savannas, can increase woody biomass, cover and tree height (Jose & Farinas, 1983; Carson & Abbiw 1990; Bond & Keeley, 2005; Higgins et al, 2007) and drive a switch in species composition. Fire protection increases the number of fire sensitive species e.g. evergreen species (Trapnell, 1959; Carson & Abbiw, 1990; Shackleton & Scholes, 2000; Plas et al, 2013), which can potentially initiate a biome switch (Bond & Midgley, 2012; Parr et al.

2012). Fire modifies the structure of woody plants and regular fires can cause a reduction in the height of woody vegetation and reduce the woody biomass and cover of an area (Higgins et al, 2007; Smit et al, 2010). Through this effect fire can impose a powerful demographic bottleneck and can prevent recruiting saplings from entering the large tree layer (Higgins et al, 2000; Lehmann et al, 2009; Prior et al, 2010).

Global Drivers of savanna change

Climate change

The global average temperature has increased by a mean of 0.85°C from 1880 – 2012, and almost the entire globe has experienced warming. Several climate change projections exist for Southern Africa based on global climate models (GCM), statistical downscalings of the GCM's and dynamical downscalings. All models concur that mean temperatures will increase up to 3°C in the next 100 years, as will the number of days exceeding 35°C (Davis, 2011). Both GCM's and GCM statistical downscaling predict increases in rainfall across south-eastern South Africa and East Africa (i.e. savannas of Southern Africa), most likely to be experienced as an increase in extreme rainfall events. However dynamical downscaling using the Conformal-Cubic Atmosphere Model (C-CAM) predicted that yearly rainfall totals will show little change in the future, with changes generally projected to be less than 10%. The central interior of South Africa is the only part of South Africa that is predicted by C-CAM to become wetter (Engelbrecht et al, 2009; Engelbrecht et al, 2013).

An analysis of the climate records for South African savanna regions, show increases in precipitation intensity in the higher rainfall savannas over the past 50 years (Kruger, 2006), but a decrease in the lower rainfall semi arid savanna regions. The lower rainfall areas have also experienced shorter annual wet spells and rain stations in the lowveld (the heart of SA semiarid savannas) have experienced a 38% decrease in annual rainfall totals since 1931 (Mason et al 1996,1999; Kruger, 2006). Regionally a trend of increasing minimum temperatures and number of hot days has been shown for Southern Africa. Extreme heat days have increased by 8.2 days since 1961 (New et al, 2004). Isolated studies from within South Africa's semi-arid savannas indicate that summer and autumn minimum temperatures have increased, as have winter maximum temperatures (Kruger *et al*, 2002). The number of hot days (30- 35 °C) and hot nights (> 20 °C) has increased since 1960 (Kruger & Shongwe, 2004; Kruger & Sekele, 2013).

Species range shifts are one of the most widely cited responses to changing climates and have been documented worldwide (Parmesan & Yohe 2003; Rosenzweig, et al. 2008; Thomas, 2010). Species are generally predicted to shift pole wards or upwards to maintain their current climatic envelope. The IPCC (2007) reports that regional temperatures have changed and will continue to cause species to shift their existing ranges. At a national scale, the most recent climate change policy document (DEA, 2011) states that species composition is likely to change in all biomes and regional changes in climate are likely to induce spatial shifts in the ranges of South African species.

Elevated CO_2

Anthropogenic activities have increased CO_2 concentrations by 40% since pre-industrial times, reaching levels that have not been experienced for the past 800 000 years (IPCC, 2013). Atmospheric CO_2 exceeded 400 ppm for the first time in 2013 having risen from pre-industrial levels of ~ 275 ppm (IPCC, 2013). Levels are projected to continue to rise and exceed 700ppm by the turn of century. Aside from driving atmospheric warming, elevated CO_2 can stimulate plant growth directly or indirectly through improved water use efficiencies. These changes are predicted to benefit savanna trees by improving growth rates or soil available water (Polley et al, 1997; Morgan et al, 2004, Bond & Midgley, 2000, Kgope et al, 2010; Donohue et al 2013; Bond & Midgley, 2012). In the mesic savannas, trees are more likely to benefit from the direct effect of elevated CO_2 and increases in tree biomass, growth rates and root carbohydrate reserves are likely (Sarmiento et al, 1985; Hoffman et al, 2000; Kgope et al, 2010; Bond & Midgley, 2012). The additional plant carbon can benefit tree saplings through increasing root carbohydrate storage, physical secondary defence and increased growth rates (Kgope et al, 2010). These changes should benefit saplings growing in the fire or browse trap by increasing resprouting rates and post burn regrowth and enhancing the probability of tree escape from the fire trap (Hoffman et al, 2000; Bond & Midgley, 2000; Kgope et al, 2010). Improved water use efficiencies caused through the indirect effects of CO_2 are more likely to benefit tree growth in more arid savannas (Polley et al, 1997; Morgan et al, 2004; Donohue et al 2013), as elevated CO_2 improves water use efficiency and increases soil available water by decreasing stomatal conductance and transpiration rates (Polley et al, 1997; Morgan et al, 2004).

A clear predicted impact of both direct and indirect effects of elevated CO_2 in savannas is an increase in woody plant encroachment. Encroachment is defined as the increase in density,

cover and biomass of woody or shrubby plants (Van Auken, 2009). Increased woody plant growth has been documented across diverse biomes of the world (Archer et al, 1995, 2001; O'Connor, 1995; Fensham & Fairfax, 2003; Wigley et al, 2009) but the increases are particularly apparent in open systems i.e. grasslands and savannas which are vulnerable to tree cover increases (Archer et al, 1995, 2001; O'Connor, 1995; Fensham & Fairfax 2003; Wigley, Bond et al. 2009). Tree cover increases in arid savannas (see Donohue et al, 2013) and mesic savannas is predicted to increase (Wigley et al, 2010; Buitenwerf et al, 2012, see Bond & Midgley 2012 for review), sometimes to the extent that biome shifts occur (Bowman et al, 2010, Bond & Midgley, 2012). Models that account for the impacts of elevated CO_2 on savanna structure predict that current trends of increasing plant biomass and woody plant dominance (Higgins & Schieter, 2009) will continue as are shifts in vegetation to alternative stable states e.g. savanna to forest (Higgins and Scheiter 2012). The combined impact of these changes promises to alter ecosystem function and ecosystem service delivery through the alteration of hydrological regimes (Asner et al, 2004), reduction of the supply of forage services (Scholes, 2003; Blaum et al, 2009; Riginos et al, 2009) and overall loss of biodiversity (Biederman & Boutton 2009; Sirami et al, 2009, Eldridge et al, 2011).

Context of the thesis

Multiple regional factors are changing in savannas; all of them have been shown to impact upon savanna dynamics. One consistent prediction through changing these drivers is that species distributions and plant abundances will also change. In this PhD I consider these two aspects

Woody encroachment

Whilst it is clear that savannas are vulnerable to woody plant encroachment there is considerable debate as to which mechanisms are driving woody encroachment with both local and global drivers being cited as the primary causes, especially in arid savannas (Archer et al. 1995; Joubert et al, 2008; van Auken 2009). Woody encroachment can be driven by land use and management practices where grazing and fire levels have been altered (Brown & Archer, 1989; Skarpe 1991; Archer et al, 1995; Heisler et al, 2004; Van Auken, 2009), but increased atmospheric CO_2 concentrations have been implicated in causing the changes (e.g. Polley 1997; Bond and Midgley 2000; Brook & Bowman, 2006; Wigley et al, 2009, Buitenwerf et al, 2012). This hypothesis is still debated because usually potential CO_2 effects are confounded by changes in land use. Thus some authors suggest that perceived changes are

simply part of the inherent variability in the system (Archer et al. 1995; Wiegand et al, 2006; Joubert et al, 2008). Regardless, the primary drivers remain unidentified as very few multi-site, multi land-use, large-scale evaluations of woody plant encroachment exist, with the majority of the studies documenting woody encroachment in areas less than $10km^2$ (Brown & Archer, 1989; O'Connor ,1995; Eckhardt et al, 2000).

Species distribution in savannas

A suite of theories exist to explain the structuring of species distributions (McArthur, 1994; Woodward, 1987; Hubbell, 2001; Gaston, 2003; Sexton et al, 2009; Holt, 2009; Chase & Leibold, 2003; Garzon-Lopex et al, 2013). The dominant framework is based on niche theory from the Hutchinson concept of the fundamental and realized niche. The fundamental niche describes the set of environmental factors that determine the space where a species could occur in the absence of biotic interactions (Hutchinson 1957; Chase & Leibold, 2003). The realized niche describes where a species actually occurs. This concept is applied almost globally as a framework to describe the geographic distribution of species (Thomas, 2010, Gaston, 2003), where the fundamental niche of plants is set by climate and edaphic factors (Cole 1986; Gaston 2003, McInnes et al. 2009). However, approaches to understanding species range limits are often correlative (Rouget, Richardson et al. 2004; Beale et al, 2008; Araujo & Peterson, 2012). Studies exploring the key factors limiting plant species distribution are rare but might be expected to include how plant demography, rates of growth, death and reproduction interact to determine the species distribution of an organism (Kearney, 2006).

The absence of detailed studies on distribution limits is most acute in the tropics where most of the world's diversity occurs (Thomas, 2010; Blach-Overgaerd et al, 2010). Authors frequently acknowledge that in the tropics the determinants of ranges are more complex (Root et al. 2003; Colwell et al. 2008; Rosenzweig et al. 2008; McInnes, et al. 2009; Thomas, 2010; Blach- Overgaard et al, 2010) and water availability and biotic interactions are increasingly important in these systems (Woodward 1987; Jolly, et al. 2005; Foden et al. 2007; Thomas 2010). There have been numerous calls for more focused studies on biotic interactions and a demographic approach to understanding species distributions (e.g. Thomas, 2010; Blach- Overgaard et al, 2010; Kearney et al, 2008; Angert et al, 2009). This approach envisions that whilst climate within the tropics may not directly impact birth and death rates, it may modify competitive interactions, which are of greater intensity in this region.

Additionally a demographic approach is necessary as the persistence of a plant may change with different demographic stages (Angert et al, 2009; Holt, 2009).

Demographic approaches in savannas are common and are essential to understanding the effect of different drivers on savanna structure and function (Hoffmann, 1999; Higgins et al, 2000; Bond & Midgley, 2001; Higgins et al, 2007; Bond, 2008; Riginos, 2009; Hoffman et al, 2009; Holdo et al, 2009; Lehmann et al, 2009; Prior et al, 2010; Werner & Franklin, 2011). However most such studies are on local populations. In savanna ecology, considerably less attention has been paid to understanding the determinants of savanna plant distributions. While several authors acknowledge that local fire and herbivory impacts can affect species composition (Dublin et al, 1990; Hoffman, 1999; Owen-Smith, 1998; Higgins, 2000; Bond et al. 2012; Staver et al, 2012), many studies only consider species distribution locally, and the implicit assumption is that at larger scales, abiotic factors such as climate and soils must be the dominant controls of distribution (Cole, 1986). Very few studies, correlative or otherwise, have explored the determinants of distribution limits of savanna plants (but see Rutherford et al, 1999).

As savannas are often structured by top-down processes and not climate, can the current Hutchinsonian niche framework of species distribution be used to understand species distributions in savannas? Clarity on this issue is essential as conservation agencies, policy makers and national agencies are making long-term management decisions based on the assumption that savanna species range shifts will be climatically controlled and that species will move pole wards or upwards with global warming (DEA, 2011; IPCC, 2007).

Outline of thesis

In this thesis, I report on two ways in which global change might influence South African savannas. The first is an analysis of historical changes in woody plant abundance at large spatial scales. I then report on studies relating to predicted range shifts of the common arid savanna tree, *C. mopane*. I selected this as a primary study species for three reasons;

1) Of the 1.5 million km^2 of Southern African savannas (i.e. Angola, Botswana, Malawi, Mozambique, Namibia, Swaziland, Zambia and Zimbabwe) (Loveland *et al* 2000), *Colophospermum mopane* (Kirk ex Benth) covers ± 555, 000 km^2 (one third) (Mapaure 1994, Timberlake 1995), making this tree a critical component of the ecosystem,

specifically due to the strong tendency of *C.mopane* to form monospecific stands (Timberlake 1995) on both nutrient rich and nutrient poor soil conditions.

2) A decade ago the South African Country Study on Climate Change (Rutherford et al 1999) predicted massive south- and westward range shifts of mopane in South Africa as a result of climate change. Because of its aggressive nature, such a range change could greatly alter the ecology of our major savanna parks.
3) It has been recorded as a bush encroaching species (Smit, 2004)

Where appropriate, I also worked on *Acacia nigrescens* in the studies. *A. nigrescens* is a deciduous, small to medium tree occurring in a wide range of soil types. This species has a wide distribution but is not as numerically dominant as *C. mopane.* While the distribution of *A. nigrescens* and *C. mopane* overlap, *A. nigrescens* does occur in wetter savanna areas.

I conducted a series of field studies, transplant experiments, lab experiments and modelling to attempt to understand the drivers of the distribution of these plants at each demographic stage. Each chapter can be read separately and in each chapter I consider how the findings could contribute to our understanding of species distribution ranges.

Chapter outlines

Chapter 2 provides an outline of the study species and the study areas. Numerous study sites were used across South Africa so I provide a general description of the north east savannas of South Africa. Detailed information on specific study areas is provided in each chapter.

Chapter 3 examines how tree cover has changed from the 1940's to 2009. Using the aerial photographic record, tree cover changes were measured across multiple land uses across the rainfall gradient with the aim of measuring the magnitude of tree cover change in different climate settings. In this chapter I attempt to untangle the role of local vs. global drivers of tree cover change.

Chapter 4 employs a typical species distribution approach based on the Hutchinson niche framework to understand which regional-scale factors are considered important in determining the distribution of this species. Such an approach allows us to a) determine the importance of environmental gradients according to a Species Distribution Model (SDM) and to compare these correlative outcomes with an explicitly demographic and experimental

approach and, b) to identify, for the rest of the study, the most important environmental factors that should be tested.

In Chapter 5 I studied the germination and early seedling establishment phases of *C. mopane* and *A. nigrescens*. As the primary factors limiting the plants at this stage are water and temperature I examined the role of these factors in limiting germination/establishment success.

In Chapter 6 I report on a transplant experiment to examine factors influencing seedling establishment and sapling success. I planted both *A. nigrescens* and *C. mopane* across a latitudinal gradient spanning 100s of kilometres from north to south. The intention was to examine plant performance both inside and outside their distribution ranges and responses to the effects of changing latitude. To examine the importance of temperature, each latitude site was paired with a higher elevation site to widen the climatic range of the transplant experiments. As biotic interactions are considered an important component in the success of a tree, saplings were planted with and without grass

In Chapter 7 I examine the ecophysiology and ecology of adult *C. mopane* using a watering experiment to explore the role of water and temperature in controlling leaf phenology, photosynthesis and productivity of this species.

Throughout the thesis the results in each chapter are considered more or less independently. I explore the possibilities of what controls the distribution limits at each demographic stage. In the concluding chapter I consider the outcomes of the study as a whole and discuss new information and insights that have emerged. The latter includes a new conceptual framework that emerged from the thesis and possible future research.

Most of the chapters were written in a format suitable for submitting to a journal resulting in some overlap among chapters.

Chapter 1: Study site

Introduction

Multiple study sites were used in this thesis, so here I provide a general introduction to the larger study area and introduce the study species *Colophospermum mopane* and *Acacia nigrescens.* Site specific detail has been included in the relevant chapters

The common setting for all of the studies was in the savannas in north east South Africa. This area incorporates the South African provinces; Limpopo, eastern Mpumulanga, and north and east Kwazulu-Natal (Figure 1). The savannas here mostly occur in three distinct savanna bioregions; the lowveld, central bushveld and the mopane bioregion (Mucina & Rutherford, 2006). The central bushveld occurs in the higher lying savanna interior, and is the coolest of the savanna bioregions. The hotter lowveld savanna occurs in the lower altitude savanna regions from the lower slopes of the escarpment though to the low lying parts in Northern KwaZulu-Natal (Zululand). The mopane bioregion covers a small area in northern Limpopo and is the hottest bioregion.

I highlight the location of the study sites on any maps in the general description.

- Black dots: Chapter 2, sites where woody cover change was measured
- Red dots: Chapter 5, location of study sites for transplant experiment across a latitudinal and altitudinal gradient
- White circle: Field site near Phalaborwa gate in the Kruger National Park. This study site was used for Chapter 6. Environmental data used in modelling exercises for Chapter 4 were from this site. Additionally part of the transect mapping in Chapter 3 was performed in this region.

General site description

Mean annual precipitation in South Africa decreases westwards from the escarpment across the interior plateau. The high elevation escarpment (separating high central bushveld and lowveld savannas) and some of the higher lying areas in Kwazulu-Natal receive the highest amount of rainfall within the general study region. There is a general gradient of increasing rainfall from the northern savanna sites to the southern savanna sites in both high and low

lying savannas (Figure 2). With increasing rainfall, grass biomass increases (Deshmukh, 1984; O'Connor et al, 2001). Rainfall is variable in savannas with the highest coefficient of rainfall variation occurring in the driest far northern savannas and decreasing with increasing latitude (Figure 4b). A temperature gradient occurs between the high lying central bushveld and low lying savanna lowveld (Schulze, 2007). Mean annual temperature (MAT) is highest along the north eastern coastal belt, the eastern border and the northern border of South Africa (Figure 3). The high-lying central bushveld savannas are the coolest savanna bioregions with a MAT of 18.4°C. The lowveld savanna and mopane bioregions are hot and have a MAT of 20.4°C and 21.4°C respectively (Mucina & Rutherford, 2006). Frost is infrequent in savannas, though it does occur in parts of the mopane bioregion (Whitecross et al, 2012) and the central bushveld. It is rare or never occurs in the lowveld savannas (Figure 4a).

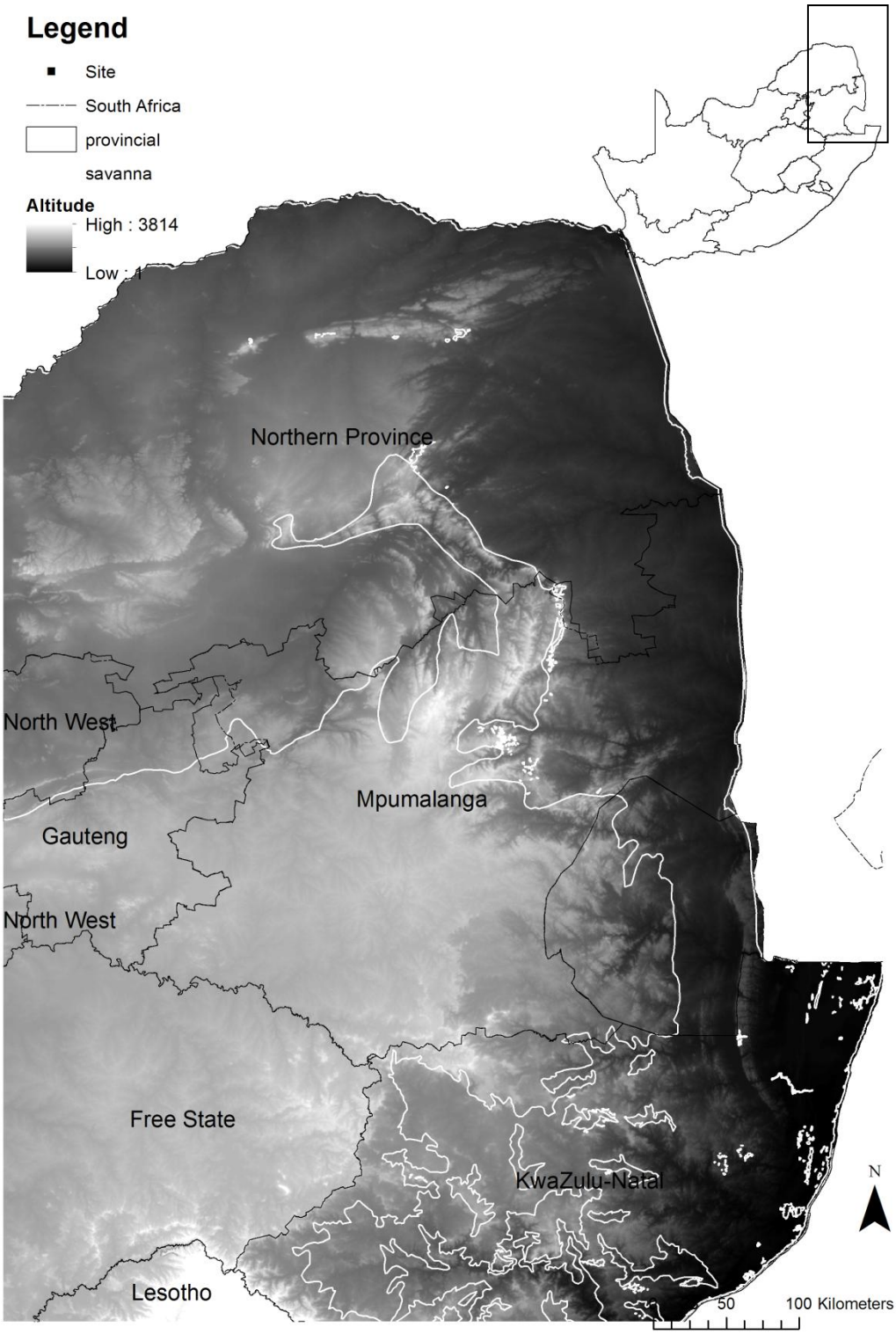

Figure 1: The distribution of savanna (dotted line) in South Africa (inset). The South African provinces are labelled. South Africa is characterised by a higher elevations in the central plateau (light colours) and lower elevations (dark colours) towards the coastal regions.

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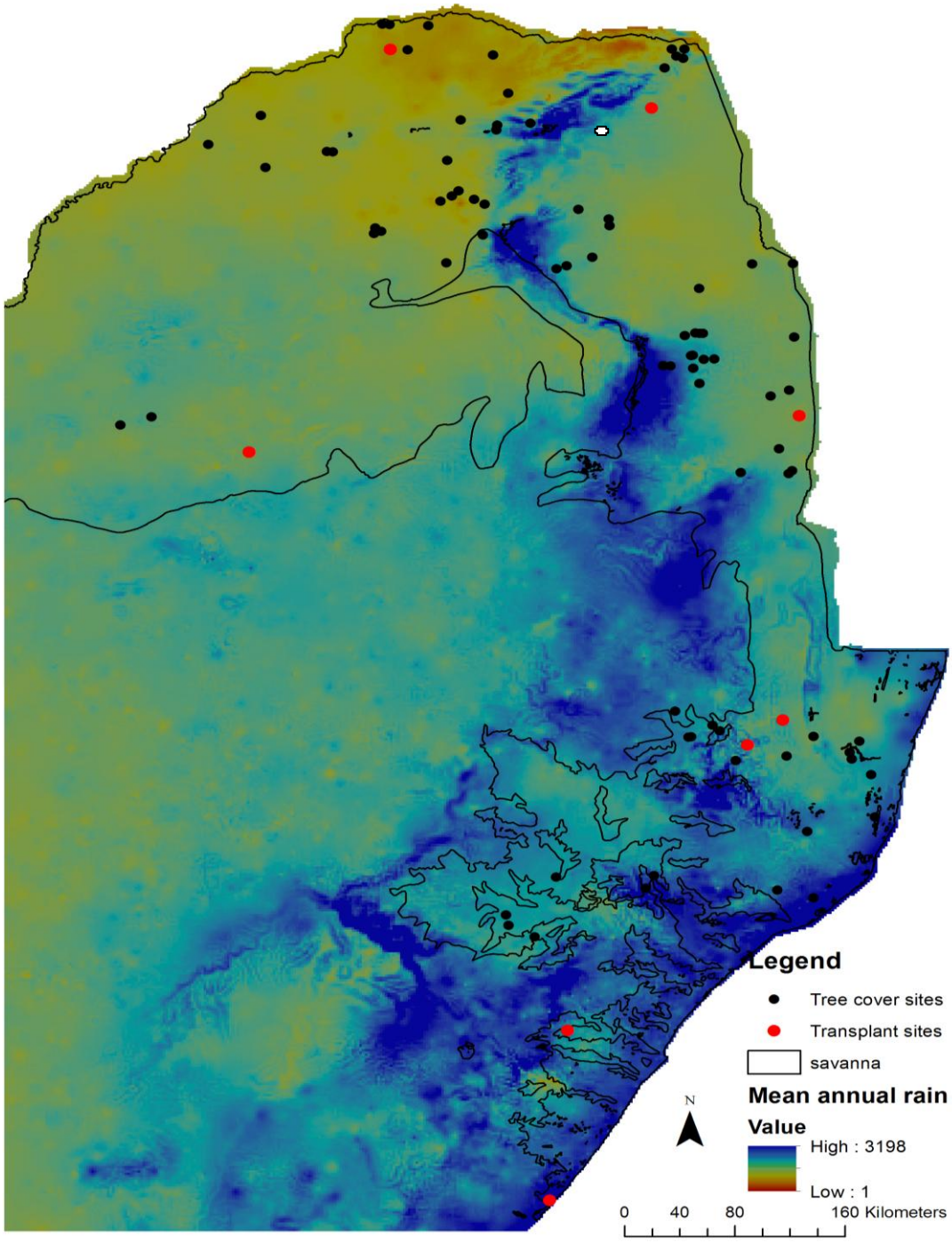

Figure 2: Mean annual precipitation (MAP) for eastern South Africa. Study sites are indicated by red points (Chapter 5) and black dots (Chapter 2). The white circle indicates the Phalaborwa site mentioned in Chapters 3 & 4). The extent of the savanna biome is outlined in the map. Dark blue indicates areas with the highest rainfall whilst brown colours indicate low rainfall. Within the savanna biome, MAP is highest in the southern savannas and lowest in the northern savannas. Rainfall data for each specific site is given in the relevant chapter.

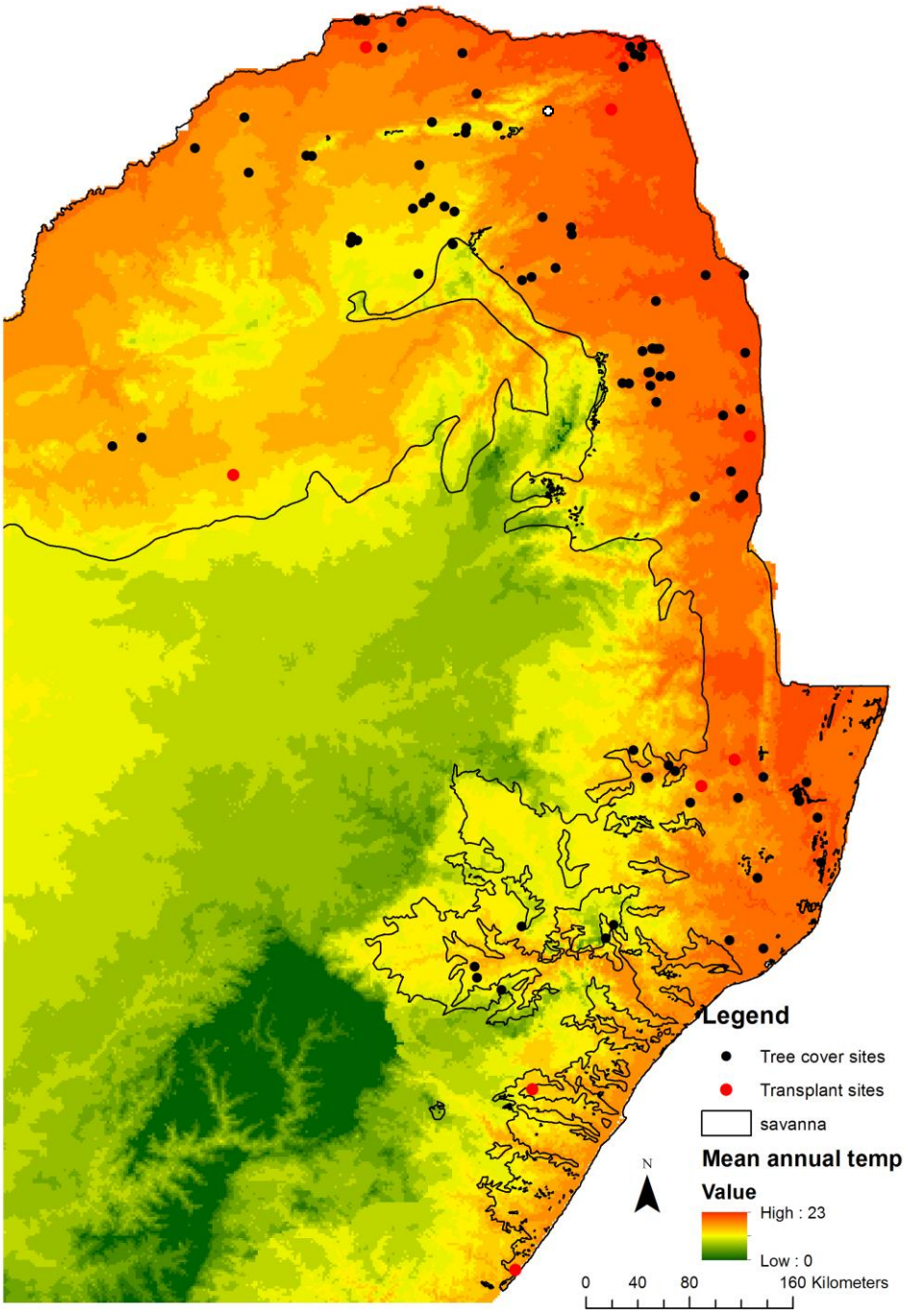

Figure 3: Mean annual temperature (MAT) for eastern South Africa. Study sites are indicated by red points (Chapter 5) and black dots (Chapter 2). The white circle indicates the Phalaborwa site mentioned in Chapters 3 & 4. The extent of the savanna biome is outlined in the map. Dark orange indicates areas with the highest MAT and green colours indicate areas with the lowest MAT. Within the savanna biome, MAT is highest in the northern and eastern border regions and coolest in the high lying central areas.

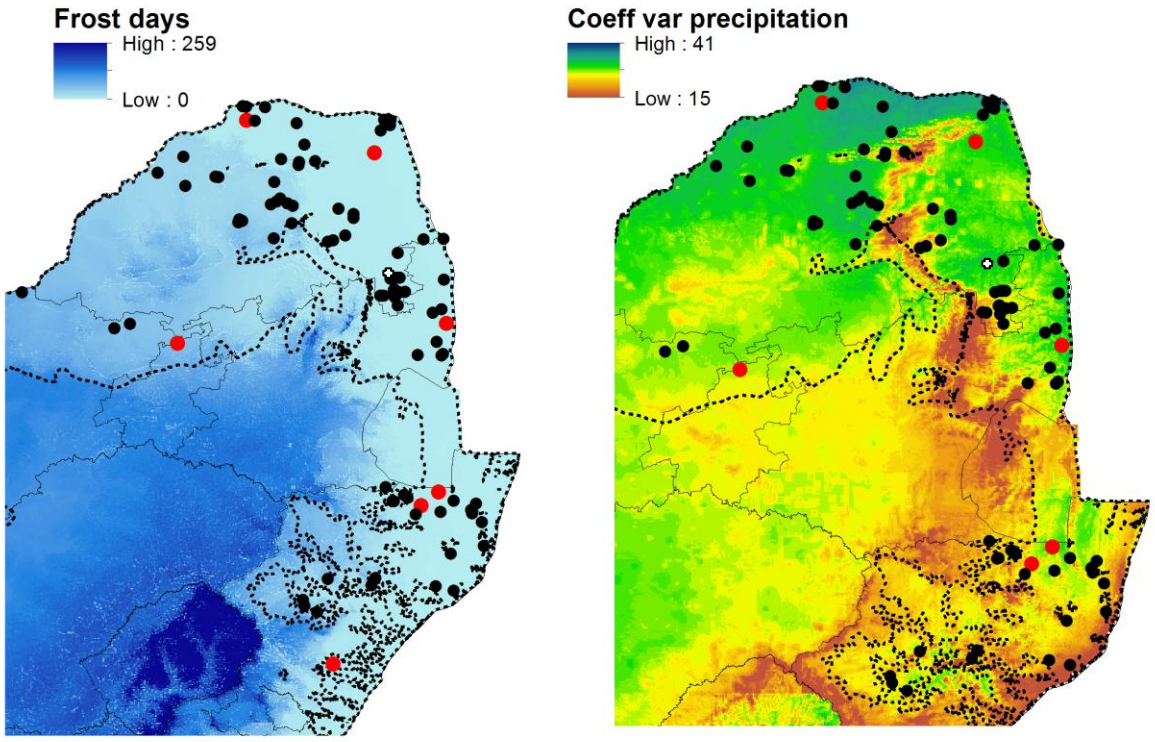

Figure 4: a) Total number of frost days per year. Frost is generally rare in savanna sites although it is relatively more common in the higher central bushveld b) Rainfall variability in savannas is high. Study sites are indicated by red points (Chapter 5) and black dots (Chapter 2). The white circle indicates the Phalaborwa site mentioned in Chapters 3 & 4. . The extent of the savanna biome is outlined in the map.

Study species

Colophospermum mopane

Colophospermum mopane (mopane) (Kirk ex Benth.) Kirk ex J.Léon is a highly dominant leguminous tree or multi-stemmed shrub, belonging to the Caesalpinoideae subfamily of the Fabaceae, (Detarieae clade) (Figure 5). It occurs in hot, low-lying regions of (sub) tropical southern Africa (Timberlake, 1995). It is a medium sized tree 4-18m in height (Figure 5). Its leaves are bifoliate with two leaflets without stalks, resembling a pair of butterfly wings. The leaves of the trees hang down during the heat of the day and the leaflets close reducing the leaf heat load. The flowers are greenish, small and inconspicuous. The fruit forms a flattened kidney shaped pod. The seeds are flat, convoluted, and sticky and dotted with resin glands (Figure 5).

It is one of the principal trees of hot, low lying areas of Southern Africa. Of the 1.5 million km^2 of the savannas in southern Africa, *C. mopane* is estimated to almost singly dominate 550 000km^2 (25-35%) of savannas (Mapaure 1994, Timberlake 1995), where it has a strong tendency to form monospecific stands (Timberlake, 1995) on both nutrient rich and nutrient poor substrates. While dominating many thousands of hectares across southern Africa, its distribution ends abruptly in South Africa, south of the Olifants River in the Kruger National Park (Palgraves, 2002). *C. mopane* has been predicted to undergo extensive south- and westward range expansion as a result of climate change (Rutherford et al, 1999). It has been recorded as a bush-encroaching species (Smit & Retham, 1998). *C. mopane* is however an important browse species in times of drought (Styles & Skinner, 1997) and has a high socio-economic value as it is used extensively for fuel wood, building material and medicine (Anthony & Bellinger, 2007, Makhado et al, 2009), and is the host of the economically important mopane worm (the larvae of *Gonimbrasia belina*), a highly-valued protein source (Timberlake 1995, Anthony & Bellinger 2007, Makhado et al, 2009).

Figure 5: a) *Colophospermum mopane* seed pods (40-50mm) and b) seeds removed from seed pods (30 – 40mm). c) Butterfly shaped leaves of *C. mopane* (30-140mm) d) 2 year old sapling, growing next to a measuring stick, each yellow: pink interval indicates 10 cm e) adult tree. (~8m)

Acacia nigrescens

Acacia nigrescens (Fabacae) or the Knob thorn is a woody tree that can grow up to 20m in height, although it usually remains between 8-10m (Figure 6). It is most common and widespread in low-altitude savannas. The leaves of *A. nigrescens* are double pinnately compound and differ from many *Acacia* species in that they are not fine leafed, but have 4-6 leaflets which are relatively long (~100 mm). Branches bear knobbly prickles and hooked blackish thorns that occur in pairs just below the nodes. The flowers are conspicuous white spikes that appear before the tree puts on its leaves in early spring. The pod is straight (~160 x 250 mm) and dehiscent. Knobbed thorns are conspicuous on the trunks of these trees although large old trees have fewer knobbly thorns.

The leaves are nutritious and the young leaflets have a low concentration of tannin and phenolics (Fornara & Du Toit, 2007). *A. nigrescens* is a favoured browse species and is heavily browsed by elephant and giraffe (Shannon et al, 2008). This heavy browsing keeps trees in a hedged state

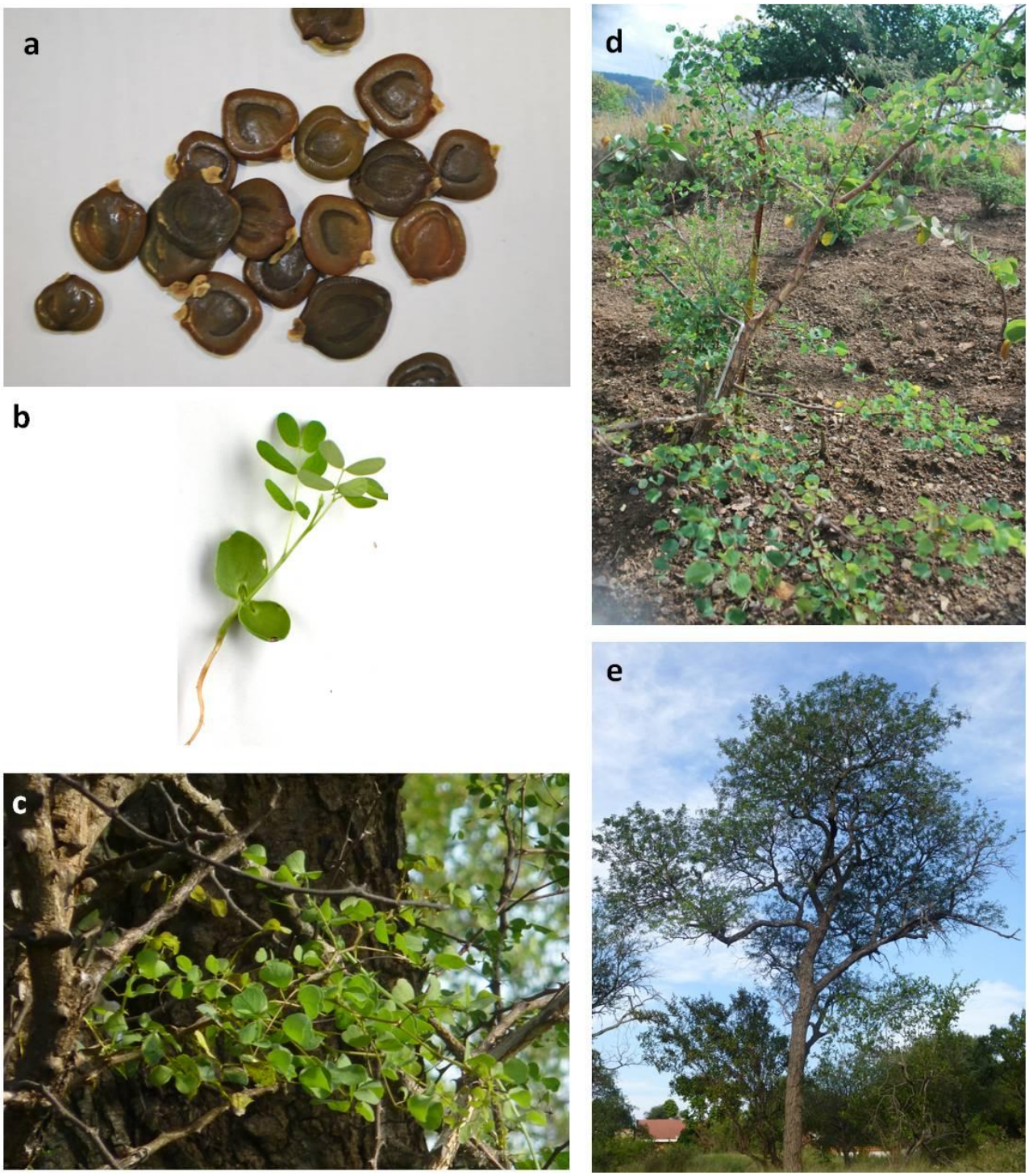

Figure 6: a) *Acacia nigrescens* seeds (10x10mm) and, b) 5 day old seedling (130 mm). c) *A. nigrescens* leaflets and branch with knobs and hooked thorns. d) 2 year old sapling, growing next to a measuring stick, each yellow: pink interval indicates 10cm. (0.8m) e) adult tree (~16m)

Both study species are widely distributed across Southern Africa. In South Africa *C. mopane* reaches its southern distribution limit with the furthest southern population occurring at in the lowveld in the Kruger National Park (Figure 7). Therefore although this species dominates

wide expanses of Southern African savannas it has a relatively restricted distribution in South Africa and occurs in a band in northern South Africa. *A. nigrescens* is widely spread in South African savannas. It does not form the dense monospecific stands characteristic of *C. mopane*, but occurs in widely spaced stands on a range of soil types. *A. nigrescens* reaches its southern distribution in the low lying savanna areas in Northern KwaZulu-Natal (Figure 7)

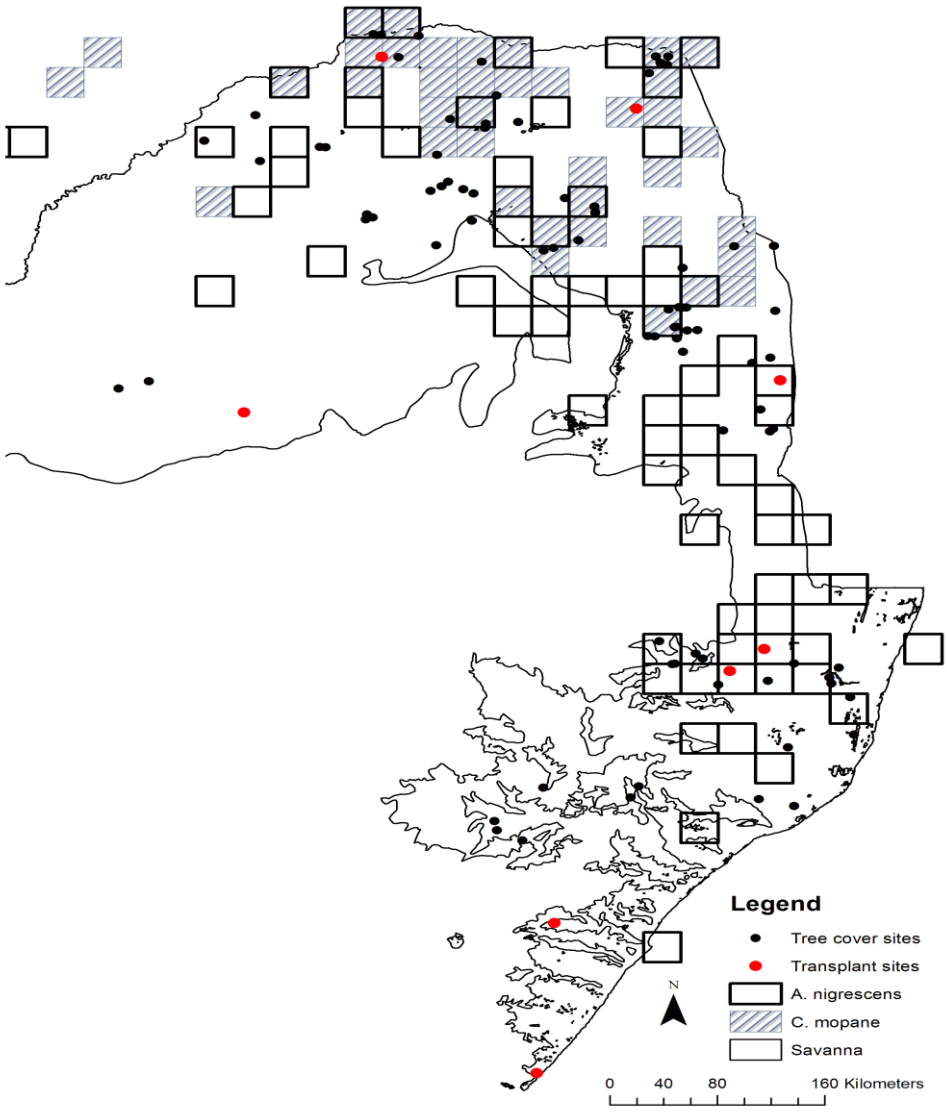

Figure 7: Distribution of *A. nigrescens* (white blocks with black outline) and *C. mopane* (striped filled boxes) across South Africa. Each block represents a quarter degree grid square (QDS) in which plants are present (SIBIS, ref). QDS's where both species occur are stripe filled with a bold black outline. The savanna biome is outlined in South Africa. Bright red dots indicate the position of the transplant sites (Chapter 5) and black dots indicate the sites were tree cover change was measured (Chapter 2).

Study site detail

Chapter 2: Woody cover change

Eighty six sites (1 site = 1 aerial photograph) were scattered across South African north east savannas across the rainfall gradient across four different land-uses (Figure 7). All transformed land was excluded from the analysis using a satellite derived landcover map of South Africa (Figure 8, white spaces; Fairbanks et al, 2000). The non-transformed areas were divided into four land-use types; conservation areas with elephants, conservation areas without elephants, commercial ranches and communal rangelands. As it is difficult to reconstruct the long-term historical land uses for all the areas, where possible we set the criteria that the present land-use was the majority use for the past 20 years.

To ensure an equal spread of sites across the rainfall gradient, the selectable areas were overlaid onto a long term rainfall map (Schulze 2007).The savanna was divided up into three rainfall areas; arid (<400mm MAP), semi-arid (400-700mm MAP) and mesic (>700mm MAP). Twenty random points were overlaid within each land-use within each rainfall zone from which to measure tree cover change. The GPS locations of the potential sites were exported to Google Earth. The area around the point was visually inspected to determine if the area was largely untransformed. The random points were used to select the aerial photos (Figure 8).

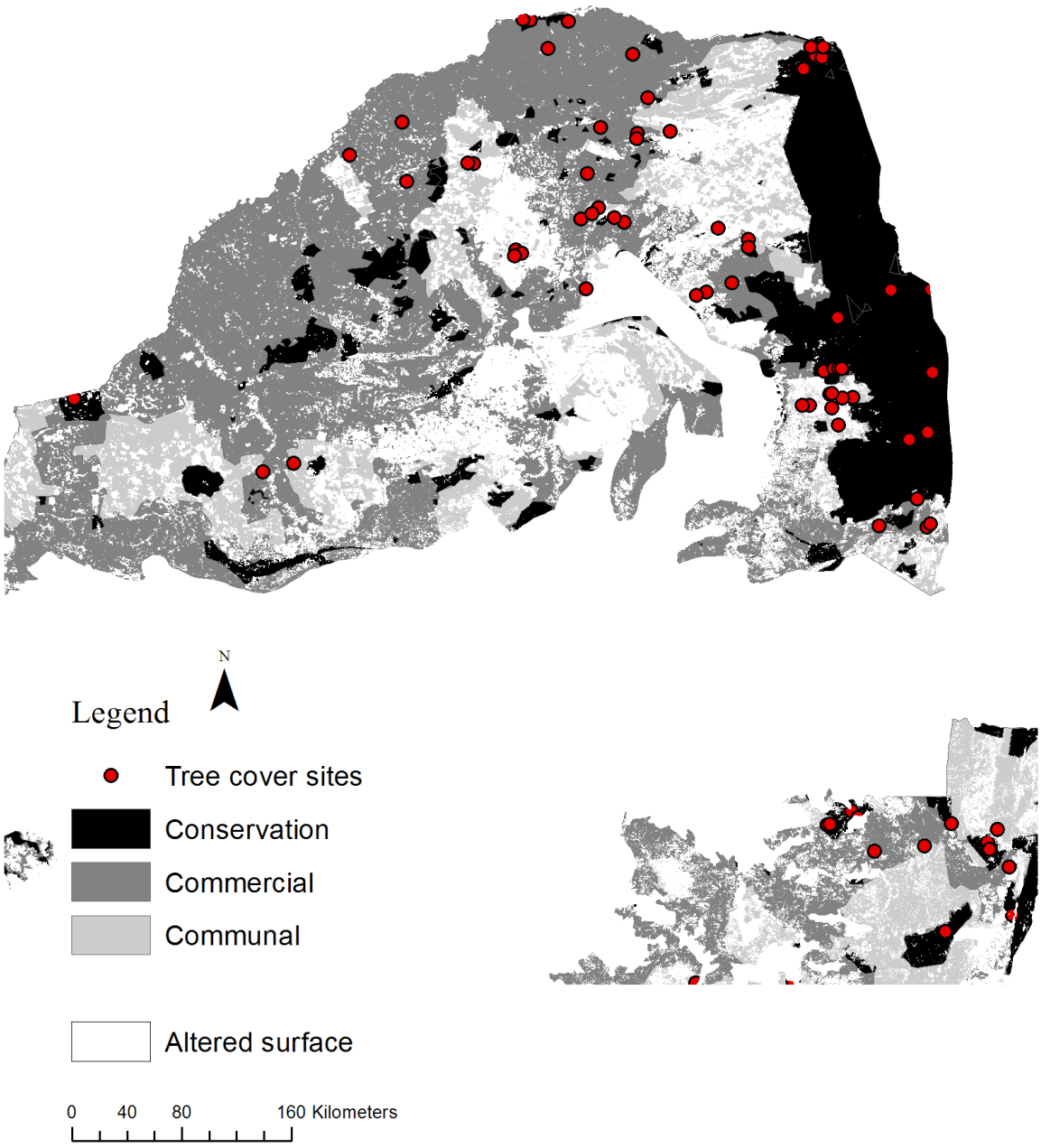

Figure 8: Distribution of aerial photos for tree cover change analyses. Transformed sites were excluded from the analysis for Chapter 2. Sites were selected from four land-uses across the non transformed savanna sites across the rainfall gradient

Chapter 5: Transplant experiment

To examine the role of climate in limiting savanna trees we established 8 transplant sites across a latitudinal and altitudinal gradient (Figure 7). Transplant sites in the maps are

indicated by the red dots on Figure 2 – 4 & 7. Details of each site are below; details of the study are in the appropriate chapter.

Figure 9: Two examples of the transplant site set up demonstrating a) two adjacent cleared plots in Tamboti Ridge site and b) an overview of the site at Simply Indigenous nursery. Cleared and non cleared plots can be observed

Punda Maria – low latitude, northern most site

The Punda Maria site was located within 2km of the village of Makuleke, 15km west of the Kruger National Park (30.95 E,22. 85 S). This area falls into the mopane bioregion and forms part of the Makulele sandy bushveld (Mucina & Rutherford, 2006). The greater area is described as variable with low mountains and slightly to extremely irregular plains to hills. The vegetation is overwhelmingly dominated by *Colophospermum mopane. Kirkia acuminata, Afzelia quanzensis* and *Combretum apiculatum* are also common. The site was positioned on a large flat plain. This is a summer rainfall region with very dry winters. In this region the MAP varies from 300 – 700mm. It is a generally frost free area. The underlying geology is gneiss (Schulze 2007; Mucina & Rutherford, 2006).

Venetia – higher latitude, northern site

This site was located near the Mopane camp inside the De Beers owned Venetia-Limpopo Nature Reserve of about 35000ha in extent. The site was located approximately 20 km south of the meeting point of South Africa, Zimbabwe and Botswana, adjacent to the Venetia Diamond Mine (29.25 E, 22.43 S). This site falls into the Mopane bioregion and the Limpopo Ridge Bushveld vegetation type. The area is flat, with sandstone as the dominant underlying bedrock beneath deep colluvial soils. Rocky sandstone outcrops interrupt the landscape. The vegetation in this area is dominated by *Colophospermum mopane* and *Commiphora glandulosa* with interspersed *Acacia nigrescens, Sclerocarya birrea* and *Adansonia digitata*

trees. It is a summer rainfall area with very dry winters from May to September. The rainy season extends between October and March, with the highest probability of rain occurring in January (Smit & Retham, 1998). The MAP is between 300 – 400mm. It is generally a frost free area, although rare frosts do occur (Whitecross et al, 2012).

Lower Sabie – low latitude, 2nd most northern site

This site was established within an old experimental plot inside the Lower Sabie rest camp inside the Kruger National Park (see Botha, 2006) (31.94 E, 25.10 S). This site falls within the lowveld bioregion and occurs in Tshokwane – Hlane Basalt Lowveld vegetation type. This area consists of flat plains with open tree savannas dominated by *Sclerocarya birrea* and *Acacia nigrescens.* It has a moderately developed shrub layer and a dense herbaceous layer. It is a summer rainfall area with dry winters and a MAP of between 400 – 800mm. The underlying geology is basalt (Mucina & Rutherford, 2006).

Kwalata – higher altitude, 2nd most northern site

Kwalata is situated in Northern Gauteng, South Africa. It is an 1800ha privately owned game farm, and forms part of the Dinokeng Conservancy (28.34 E, 25.39 S). It falls into the Central Bushveld bioregion and the vegetation is classified as Springbokvlakte Thornveld. This is a low thorn savanna occurring on flat to slightly undulating plains. Trees occurring in this area are *A. karoo, A. luederitzii, A. nilotica* and tall shrubs *Dichrostachyus cinerea* and *Grewia flava* (Mucina & Rutherford, 2006). The altitude in this vegetation type ranges from 900-1200m, and the rainfall is characterised by a summer rainfall and very dry winters. Infrequent frosts occur in winter. The long term mean rainfall for this greater region is 500-650mm with a mean annual temperature of 18.5. The underlying geology consists of ecca shales.

Tamboti Ridge – low altitude, 3rd most northern site

This site was established in a private farm in an old abandoned field used to graze cattle (31.83 E, 27.37 S). The site falls within the lowveld bioregion and the Zululand lowveld vegetation type. This area is an extensively flat landscape supporting dense thickets of *Dichrostachus cinerea* through to park like savanna with flat topped *A. tortilis* to tree dominated woodlands dominated by *Sclerocarya birrea*. Common trees in this area are *A. burkei, A. nigrescens* and *Schlerocarya birrea.* This is a summer rainfall area with some rain in winter. The MAP is about 500- 900mm. It is generally a frost free area. The geology in this area consists of shales (Mucina & Rutherford, 2006)

Malan – higher altitude, 3rd most northern site

The site was established on a private cattle ranch, near Magudu between Pongola and Vryheid (31.57 E, 27.54 S). The site falls into the lowveld bioregion and the Northern Zululand sourveld vegetation type. The dominant structural vegetation type is wooded grassland. The terrain is mainly low, undulating plains and hills. It is a summer rainfall area with a little rain in winter. The MAP ranges from about 600 – 1050 mm. Frost rarely occurs in the region. Common trees in the area are *A. sieberiana, A. nilotica* and *A. tortilis.* The geology consists of dwyka formations (Mucina & Rutherford, 2006).

Simply indigenous – low altitude, southern most site

The site was situated on a private farm in the hills above the coastal town of Port Shepstone (30.68 E, 30.3 S). The area is used as a nursery and the larger site was not severely transformed by grazing or cultivation. It is situated in the Coastal belt bioregion. The vegetation in this site is classified as Kwazulu-Natal Coastal belt thornveld. This broader vegetation type occurs on a landscape described as a highly dissected area with undulating coastal plains. The grassland is dominated by *Themeda triandra* interspersed with acacias. It is a summer rainfall area, with some winter rainfall. MAP ranges between 740mm – 940mm. Summers are hot and humid and winters are mild. Frost does not occur in this area. The area is underlain by Margate granites (Mucina & Rutherford, 2006).

uKulinga – higher altitude, southern most site

uKulinga is situated in the sub-escarpment savanna bioregion. uKulinga is the experimental farm of the University of Kwazulu- Natal. The site is situated ~5km from the provincial capital, Pietermaritzburg (30.37 E, 29.63S). The plots were established in untransformed area within the experimental farm. The site falls into the sub-escarpment savanna bioregion and the vegetation is classified as KwaZulu-Natal Hinterland Thornveld, where the vegetation is open thornveld dominated by *Acacia* spp. found on undulating plains on the upper margins of river valleys (Mucina & Rutherford, 2006). Common trees are *A. robusta, A. nilotica,* and *Erythrina latissima.* It is in a summer rainfall area with some rain in winter. MAP ranges between 650 – 1000mm although the long term mean annual rainfall for this site is 838mm. Winters are mild with occasional frost. Soils are derived from shales and are fine textured (Fynn et al, 2003).

Chapter 2: Widespread woody cover increases over 70 years suggest CO_2 and not land use as a driver

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NS designed the study , performed the analysis and wrote the mauscript WB, SA, BE are supervisors and provided advice and commented on the manuscript, SA provided funding, BE provided technical expertise and access to facilities to conduct analysis

Abstract

Increasing woody cover and biome shifts in "open" systems are occurring globally. Both local and global drivers, particularly elevated CO_2, have been implicated in the woody cover increases. The debate on their relative importance remains unresolved as very few multi-site, multi land-use, large-scale evaluations of woody plant encroachment exist. We compared tree cover change across four very different land uses (commercial ranching, conservation with/without elephants and communal rangelands) in South African savannas. These land-uses, across the rainfall gradient, form a natural experiment from which to investigate the magnitude and trajectory of tree cover change. They also provide the opportunity to tease apart the importance of local versus global drivers of tree cover change. Each land use should have different trajectories of tree cover change, unless a global driver is causing the increases. Tree cover change was measured between 1940 and 2009 using the aerial photo record. Detection of woody cover from each aerial photograph was automated using eCognitions' Object based image analysis (OBIA). Tree cover increased in all land uses across the rainfall gradient, except in the presence of elephants in the low rainfall areas. Tree cover in the low rainfall areas frequently exceeded the maximum tree cover threshold that is predicted for African savannas. Our results suggest that elevated CO_2 is driving an increase in tree cover across South African savannas. The widespread increase highlights the vulnerability of the economically important savanna regions to the negative ecological and economic impact of woody encroachment.

Introduction

Woody cover is increasing and biome boundaries are shifting (Bond & Midgley, 2012). In recent decades these increases have been documented globally (O'connor & Roux, 1995; van Auken, 2000; Fensham & Fairfax, 2003, Wigley et al, 2010), across almost all biomes [(forests (Coop & Givnish, 2007), grasslands (van Auken, 2000), tundra (Stow et al, 2004), savannas (Wigley et al, 2010)]. Yet the biomes most vulnerable to encroachment are the "open" systems, like savanna and grasslands (Archer et al, 1995, 2001; Bond & Midgley, 2000; Bond & Midgley, 2012). Although widespread woody cover increases occur in these systems, the scale and magnitude of change is not known, and underlying drivers are still debated. Controversially, widespread woody increases have been atributed to global drivers (Buitenwerf et al, 2011; Bond & Midgley, 2012; Donohue et al, 2012), where elevated CO_2

and changes in rainfall regimes (Kulmatiski & Beard, 2013) have been cited as the primary cause. More commonly, woody cover increases have been attributed to land use caused by the local scale management (Brown & Archer, 1988; Archer et al, 1995; Roques et al, 2001; Skarpe, 1990)

Land managers in rangelands frequently alter fire and herbivory regimes to achieve management outcomes, which can strongly influence the trajectory of woody cover change. Sustained heavy livestock grazing can reduce above and below ground grass biomass (Holland & Deetling, 1990) which increases rooting space and soil moisture availability for woody plants (Skarpe, 1990). Coupled with a reduction in fire frequency and intensity (Norton – Griffiths 1979; Roques et al, 2001; Bond, 2008), woody plants experience greater seedling survival, growth rates and an improved escape probability from the fire trap (Scholes & Archer, 1997; Bond, 2008; Fensham and Fairfax 2009). On the other hand browsers (ranging from goats to elephants) can suppress woody growth (Dublin et al, 1990; Scholes & Archer 1997; Sankaran et al, 2008, Staver et al 2009), limit the establishment of woody seedlings (Prins & van der Jeugd 1993), reduce canopy cover and the rates of increase of bush clump diameter (Hester et al, 2005). The recent widespread elimination of megafauna e.g. elephants, and the overall reduction in the numbers of browsers, (Owen-Smith, 1992; Bond & Midgley, 2000; Bond, 2008) should be considered as an alternative driver of wide scale tree cover increases in Africa. This is, however set against a backdrop of increasing human densities which exert a heavy pressure on woody resources through harvesting and subsistence activities (Banks et al, 1996; Bucini & Hanan; 2007) to the extent that widespread decreases in woody cover are expected for several areas (Wessels et al, 2013).

At a global scale elevated CO_2 is proposed to drive increasing woody plant dominance, although the mechanisms differ between low and high rainfall savanna areas. In low rainfall systems where water is the main limitation to growth, elevated CO_2 can enhance plant water use efficiencies (WUE) by reducing stomatal conductance and transpiration (Donohue et al, 2013; Ainsworth & Long, 2005; Polley et al, 1997). This can improve seedling survival and plant growth rates. However, the degree to which this will benefit grasses and alter the tree: grass interactions in these systems is not known. The second mechanism depends on the direct effects of CO_2 fertilization on photosynthetic rates and may be particularly prominent in fire-dominated mesic savannas, where plants have a carbon sink in the form of stored root reserves to escape the flame zone (Bond & Midgley, 2000; Schutz et al, 2009). Here elevated CO_2 will favour the regrowth of juvenile trees trapped in the fire trap (Bond & Midgley,

2000), through increasing root carbohydrate acquisition. The enhanced root reserves can accelerate height growth, increasing tree escape probabilities from the fire trap (Schutz et al, 2009). Increases in mean annual rainfall, and changes in rainfall intensity (Good & Caylor, 2011; Kulmatiski & Beard, 2013) in water limited 'stable' savannas (Sankaran et al, 2005, Good & Caylor, 2011) have been suggested to be an important additional global climate driver influencing tree cover change.

Several recent regional scale studies on tree cover in African savannas form a theoretical framework from which we can conceptualize the process of woody cover change (Bucini & Hanan, 2007; Sankaran et al, 2005; Staver et al, 2011). In low rainfall savannas (MAP < 650mm), tree cover is limited by water availability and the woody encroachment potential is small. Although herbivory and fire act to keep tree cover below the maximum threshold (Bucini & Hanan, 2007; Sankaran et al, 2008), maximum tree cover is low and reaches a low maximum tree cover threshold that is constrained by water availability (Sankaran et al, 2005) (Figure 1). Given the water limitation, the impact of CO_2 fertilisation is expected to be measureable here (Figure 1) and elevated CO_2 should increase the maximum tree cover threshold (definition per Sankaran et al, 2005), where the maximum tree cover, for the same amount of rainfall, increases (Figure 1). In the high rainfall savannas there is sufficient water for canopy closure (Sankaran et al, 2005, Bond, & Midgley, 2012), and fire, herbivory and human disturbance become the primary determinants limiting tree cover. Thus in these 'unstable' savannas the potential for a greater magnitude of woody encroachment is high as the maximum tree cover threshold is high (i.e. 80% tree cover = forest). These areas are therefore also vulnerable to biome shifts as grass production rapidly declines when woody cover exceeds a threshold between 40-50 % (Scholes, 2003). At high tree cover, grass fuel loads are reduced and fires in turn are excluded from the system (Archibald et al, 2009; Staver et al, 2011), altering ecosystem function and initiating a potential biome switch towards a closed canopy forest. Thus increases in cover, exceeding 40%, offer a warning of a potential biome switch.

South African savannas are commonly exposed to four very different land uses (commercial ranching, conservation with elephants, conservation without elephants and communal rangelands), each with very distinct management characteristics. These multiple land-uses across the savanna rainfall gradient form a natural experiment from which to investigate the magnitude and trajectory of tree cover change, offering the opportunity to tease apart the importance of local versus global drivers on tree cover changes. Each land use should have

very different trajectories of tree cover change (Scholes, 2003). Communal rangelands are home to subsistence farmers in rural villages, who run herds of goats (browsers) and cattle (grazers). A heavy harvesting pressure on the woody component is predicted to result in 'deforestation' (Table 1) (Banks et al, 1996, Wessels et al, 2013). Tree cover increases are predicted for commercial ranches as they are dominated by grazers (cattle) and fires are often suppressed. Conservation areas are the closest 'control' systems available; here, the natural processes of frequent fires and moderate herbivory (grazers and browsers) are mostly maintained. A convenient distinction between conservation areas is the presence or absence of elephant, a difference that enables us to test the impact of this single agent on tree cover change (Table 1).

Table 1: Land use management characteristics, and their expected outcome on woody cover change in South Africa

Landuse	Mean no. years between fires	Human population	Grazer density (kg/ha)	Browsers	Elephants	Overall change
Commercial	4	722759	36.0	No	No	Increase
Communal	5	10.67 million	49.1	Yes	No	Decrease
Elephants	2	20952	30.5	Yes	Yes	Decrease
No elephants				Yes	No	No change
Reference	Archibald et al, (2009)	(www.census2011.ac.za)	Global Livestock Distributions 3 arc min (FAO, 2005) filled using (Fritz & Duncan, 1994) and unpublished data (see Archibald et al, 2009)			

We used this natural experiment in the north-eastern savannas of South Africa to:

1. Quantify the magnitude and direction of tree cover change using the aerial photograph record across a multi-site, multi land-use, regional-scale study of woody plant change over the past 70 years.
2. Determine the differences in woody cover change across four different land use types in both low and high rainfall savannas with the expectation that
    a. If land use is driving tree cover change, we expect different trajectories of tree cover change across each land use (see Table 1 for predictions), the magnitude of each modified according to the rainfall.
    b. If atmospheric CO_2, or another global driver is impacting tree cover change, then woody cover increases will occur across all land use types.
3. As arid systems offer the potential to measure CO_2 effects on potential tree cover, we examined the changes in maximum tree cover in arid savannas (<650mm MAP).
    a. If CO_2 fertilisation is acting upon tree cover in the low rainfall areas, we expect that there will be an increase in the number of sites that exceed the maximum tree cover threshold defined for African savannas over the historical record (Sankaran et al, 2005) (Figure 1).

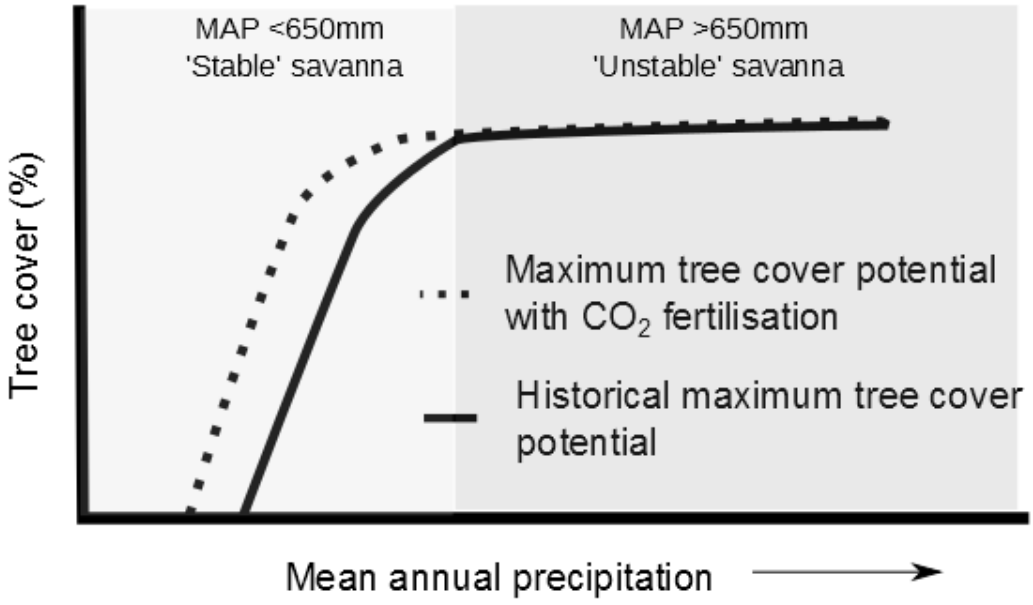

Figure 1: Current defined limits of maximum tree cover (as defined by Sankaran et al, 2005) (solid black line) across a rainfall gradient. Maximum tree cover in low rainfall savannas (MAP <650mm) is constrained by water availability. CO_2 fertilisation is expected to increase the maximum tree cover, for the same amount of rainfall

Methods

Site selection

Each site consisited of an aerial photograph pair; the earliest available photograph and a photograph from 2010. We restricted the selection of sites to South African savannas. Using a GIS (ESRI, 2011) we contained the analysis within the savanna biome (Mucina & Rutherford, 2006). All transformed land was excluded from the analysis using a satellite derived landcover map of South Africa (Fairbanks et al, 2000). The non-transformed areas were divided into four land-use types; conservation areas with elephants, conservation areas without elephants, commercial ranches and communal rangelands. As it is difficult to reconstruct the long-term historical land uses for all the areas, where possible we set the criteria that the present land-use was the majority use for the past 20 years. The communal rangelands were set aside in 1913 with the passing on the Native Land Act, additional "homeland" areas were added in 1936 (passing of the Native Trust and Land Act), and thus this landuse has remained stable for the duration of the study period. The history of formal conservation areas is also well documented and readily accessible.

Conservation sites were selected using several spatial databases; (SANPARKS, World database of conservation areas (www.wdpa.org,) Vegmap (Mucina & Ruthford, 2006) and De Beers database of protected areas), representing both formal and informal conservation areas. The complete database of protected areas was joined and each area was assigned a classification of elephant present or absent. This classification was made using local expert knowledge, information from the internet and site visits. Communal areas were selected from land tenure maps.

To ensure an equal spread of sites across the rainfall gradient, the selectable areas were overlaid onto a long term rainfall map (Schulze 2007).The savanna was divided into 3 rainfall areas; arid (<400mm MAP), semi-arid (400-700mm MAP) and mesic (>700mm MAP). Twenty random points were overlaid within each land-use within each rainfall zone from which to measure tree cover change. The GPS locations of the potential sites were exported to Google Earth. The area around the point was visually inspected to determine if the area was largely untransformed. The random points were used to select the aerial photos (Figure 2).

Measuring tree cover change

The aerial photographic record from 1937-1956, covers the extent of the savanna region and represents the first near complete aerial photograph coverage of the savanna. The aerial photograph flight plans were digitized and geo-referenced using ARCMAP 10 (ESRI, 2011). The flight plans map the location of every aerial photograph, providing each photo with a unique reference code. The random points were overlaid onto the flight plans and the appropriate aerial photographs in this early period were selected. If a random point fell on an aerial photograph with a scale smaller than 1:25000 it was excluded from the analysis.

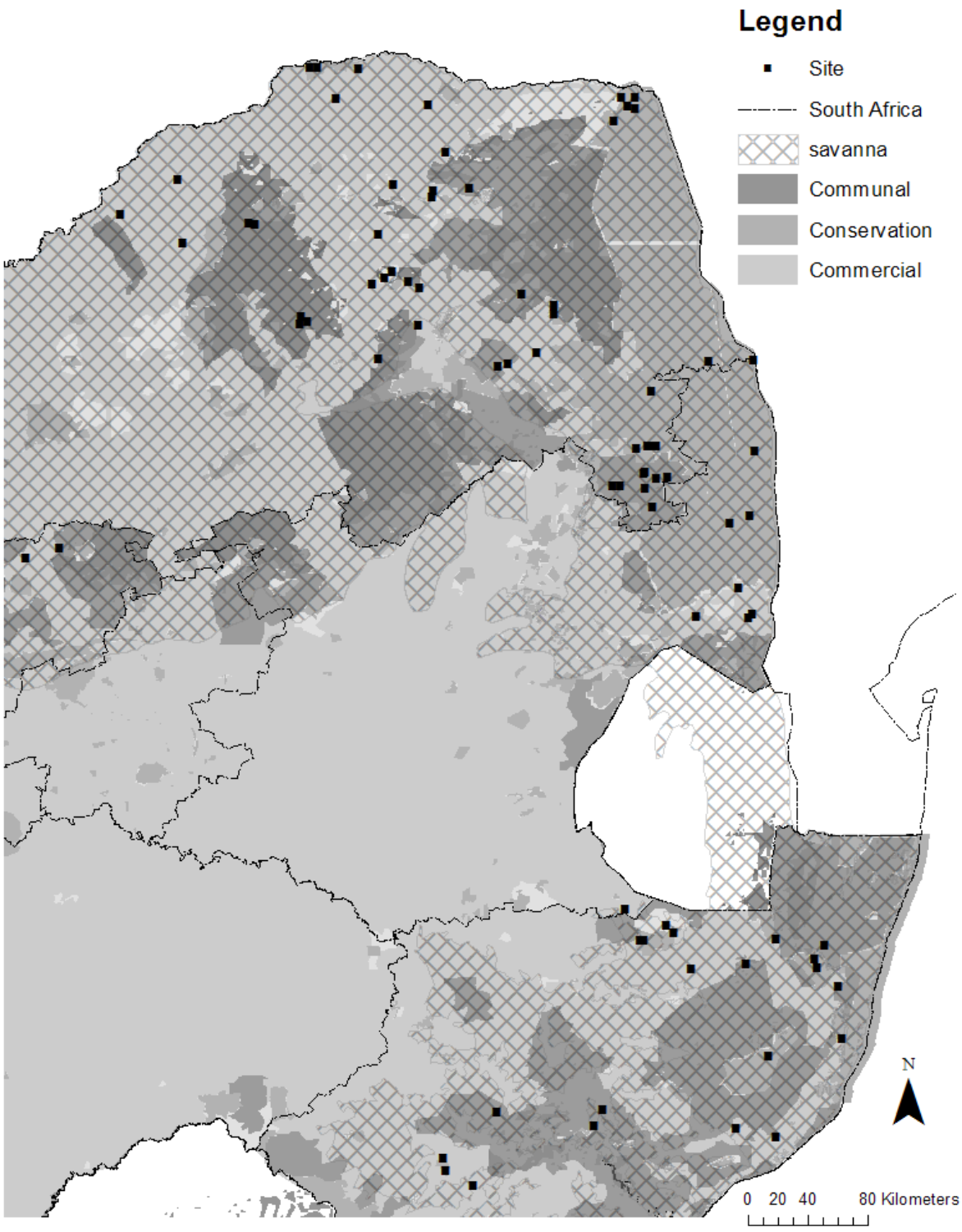

Figure 2: Site map, showing positions of 84 aerial photograph pairs in the savanna biome of South Africa. Hatching indicates the limits of the savanna biome. The shades of grey indicate the different land-uses. Conservation areas in this map are not separated out by elephant and non elephant.

The selected aerial photograph negatives were ordered from the Chief Directorate: National Geo-spatial Information (Mowbray, Cape Town, RSA). The negatives were scanned at a high resolution of 600dpi. The 2009-2010 aerial photographs were used to quantify vegetation change since 1937-1956. These were orthorectified 2009 colour images (0.5m). Using the 2009 images and the flight plans for reference, the 1940's aerial photographs were geo-referenced and orthorectified using ERDAS Imagine 11. All photographs were clipped to remove black borders, and were orthorectified using a minimum of 5 manual tie points using polynomial 3rd order geometric model. The orthorectification was accepted if the RMSE was less than 4.0. The 1940's photographs were subject to image equalization and brightness adjustments to maximize tree visibility. Each aerial photograph pair was then opened in eCognition Developer 8. eCognition Developer is a program used to recognize objects from images, and was used to automate tree detection from the aerial photographs, thus allowing a large area coverage. Each image was segmented using multi-resolution segmentation which divided the photograph into homogenous regions based on compactness and shape attributes of neighbouring pixels. The images were segmented into objects at fine scale of 14 which produces small homogenous units sufficient to identify trees and a large scale of 200 producing landscape wide homogenous units e.g. identified burn scars and fields. The shape value, which defines the weight shape when segmenting the image, was set at 0.1; the higher the value the lower the influence of colour on the segmentation procedure. The compactness criteria were set at 0.5 where the higher the value the more compact the objects. To aim for a high level of accuracy five percent of the image (calculated as 5% of pixels) were classified manually into trees and grass. A feature space optimization was run using 30 variables to classify the objects into either trees or grasses, based on the colour, shape, texture and size of objects as well as their context and relationships between each other within and across scales. The variables that resulted in the highest separation distance were used to automatically classify trees and grasses for the entire extent of the image. After classification was complete the accuracy was assessed using the built in accuracy assessment of eCognition. One hundred tree and grass objects were manually selected. The manual classifications were compared to the automated classifications. If the accuracy was less than 90% then more manual points were added and the images were re-classified. Accepted classifications were exported as rasters to Arcmap 10 (ESRI, 2011) and were visually compared to the aerial photographs.

The accepted classified rasters were overlaid onto the aerial photographs and small transformations to the areas e.g. roads and small fields were clipped and removed from both

old and new images. The rasters were used to assess tree cover change from the 1940's. The percent tree cover change was assessed using zonal statistics in Arcmap 10 (ESRI, 2011). Tree cover was assessed as the total number of tree pixels of all the pixels in the image. A total of area ~800km^2 was analysed and assessed for tree cover change.

Data analysis

All data were analysed using R 3.0 (R Core Team, 2013). Data was normally distributed and remained untransformed. An ANCOVA was performed to determine the role of land use in driving tree cover changes across the rainfall gradient. Important environmental variables that also vary across this rainfall gradient were included as covariates (see Table 3). The covariates were assessed for high levels of correlation before they were analysed. Altitude was highly correlated with mean annual temperature and was therefore removed from the analysis (see Table 2 for list of all covariates). Rainfall was categorized into high rainfall (MAP> 650mm), and low rainfall (MAP<650mm), these categories were selected to correspond with the rainfall at which the stable: unstable savanna divide occurs (Sankaran et al, 2005). A stepwise procedure using the STEP function in R was used to determine which combination of factors produced the best model fit. Paired t-tests were used to determine if woody cover increases were significant for each separate land use in both high and low rainfall savannas.

Table 2: Environmental covariates included in the ANCOVA

Environmental covariable	Source
Frost	Schulze (2007)
Mean annual rainfall	Schulze (2007)
A-pan evaporation	Schulze (2007)
Altitude	Schulze (2007)
Mean annual temperature	Schulze (2007)
Starting tree cover	1940 tree cover from aerial analysis

To place our data in a regional context we compared our data points to the equation developed by Sankaran et al, (2005), which describes the upper bound of tree cover in low rainfall areas by a 99th quantile piece-wise linear regression, with a 650mm MAP

breakpoint. As trees are typically absent below 101mm MAP, the equation for the line quantifying the upper bound on tree cover occurs between 101 and 650 mm MAP (Equation 1). At higher rainfall sites maximum tree cover is bounded at 80% tree cover.

$$\text{Tree Cover (\%)} = 0.14(\text{MAP}) - 14.2. \quad (1)$$

We plotted the 1940 tree cover against rainfall, restricting the analysis to areas with rainfall below 650mm. As we are comparing tree cover values derived from aerial cover measurements against tree cover values mostly based on ground measurements, tree cover of our sites will be slightly higher due to the difficulty or removing shadows entirely from the edge of the classified tree. Therefore we fitted a 95th quantile to our data and compared the linear output to equation (1) (Figure 3). The equation intercept of the1940 data (y intercept = 13.7), and the slope (0.138) closely match the fit to that of Equation (1) (Figure 3), thereby allowing us to relate changes in woody cover at our sites to that of established theory.

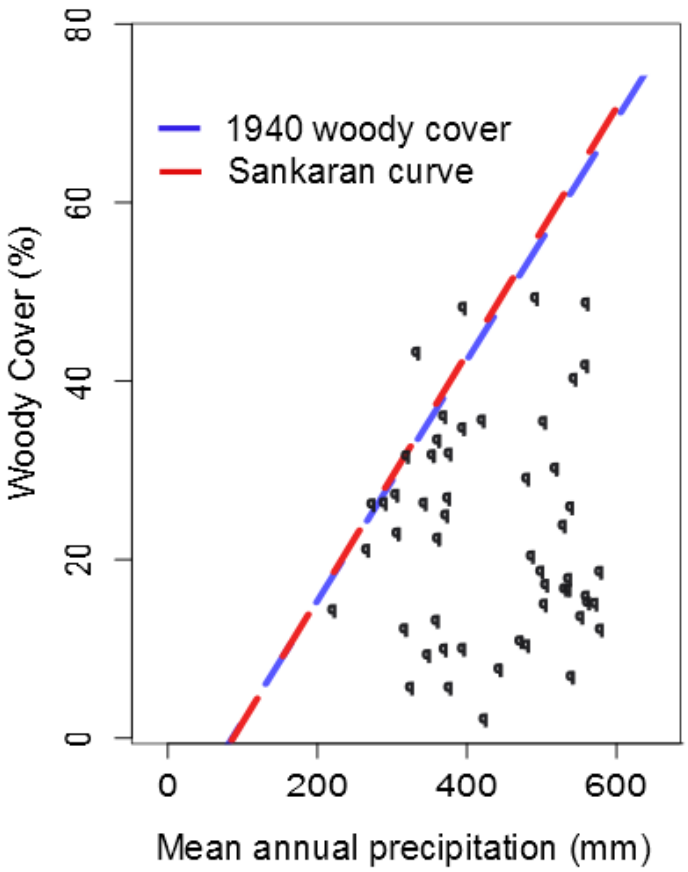

Figure 3: Comparison of the quantile linear regression of Sankaran et al, (2005) (red line) and our 1940 tree cover data points (blue line).

Results

Magnitude of total tree cover change

Total woody cover increased in three of the four land use types from the 1940's to 2009 (repeated measures ANOVA $F(3,145) = 857.92$ $p < 0.001$). Overall total tree cover increased by 11.15% in commercial areas (total area = 248km^2), 15.54% in communal areas (total area= 216km^2) and 16.84% in conservation areas without elephants (70.7km^2). No change (0.33%) occurred in total woody cover in conservation areas with elephants (302 km^2).

Landuse and tree cover change

Average woody cover increased at low and high rainfall sites and across all land use types from the 1940's to 2009 – the one exception being the low rainfall conservation areas with elephants (Figure 4). Paired t-tests confirmed, with one exception, that tree cover increases were significant (Table 3). On average, in arid commercial areas tree cover increased by 38% from 27% to 38%, , while mesic commercial areas experienced a 68% increase in tree cover from 25% to 44%. Communal rangelands experienced the greatest increase in cover in both low and high rainfall savannas. Cover doubled from 17.5% to 35% in low rainfall areas and by 266% from 12% to 44% in high rainfall areas. In arid conservation areas when elephants were not present a 44% increase from 30% to 42% occurred. In the high rainfall savannas of the same land landuse type a 56% increase in tree cover from 37% to 43% occurred. In the low rainfall savannas, elephants prevented tree cover increases (a net decrease of 1.4%, from 34.2% to 33.7%). However in high rainfall savannas, a 55% increase in tree cover from 19.9% to 58% was recorded.

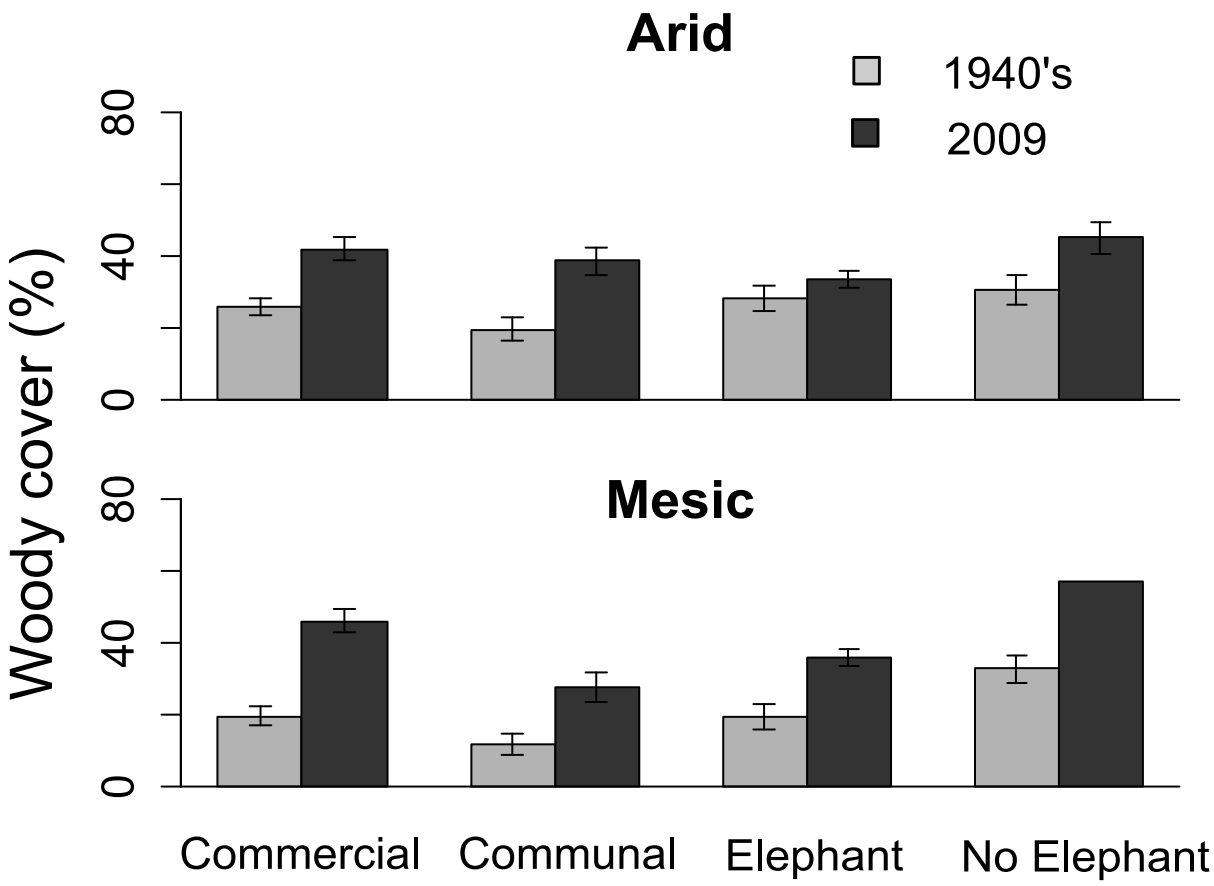

Figure 4: Woody cover increased significantly at low (MAP<650mm) and high (MAP>650mm) rainfall sites and across all land use types from the 1940's to 2009 – the one exception being low rainfall conservation areas with elephants which showed no significant change since the 1940's. Bars indicate standard errors, n=86.

Table 3: Paired t-tests comparing changes in woody cover across four land uses between 1940's and 2009. Elephants prevented tree cover increases in the low rainfall savannas.

	Arid (MAP < 650mm)			**Mesic (MAP > 650mm)**		
	t	Df	*P*	t	df	*P*
Communal	-7.370	14	*P*<0.001	-5.24	10	*P*<0.001
Commercial	-5.061	17	*P*<0.001	-2.804	4	*P*<0.05
Elephants	**NS**			-4.201	4	*P*<0.01
No elephants	-2.87	4	*P*<0.05	-3.733	5	*P*<0.05

An ANCOVA with a combined model of land use, rainfall and the environmental covariates (starting tree cover and mean annual temperature) only explained 34% of the variability in tree cover changes (ANCOVA F=7.981, $df_{6,74}$ $p<0.001$) (Table 3). In this model, of the four land uses, only elephants had a significant influence on the degree of woody cover change (t value = -4.187, p=0.00). Rainfall, starting tree cover and mean annual temperature were factors that affected the vulnerability of the area to change. Wetter and warmer areas were more prone to increases in tree cover. The higher the starting tree cover (ie 1940 tree cover) the lower the potential for tree cover increase (Figure 5). When initial tree cover exceeded 20%, the likihood of a large tree cover increase declined. When tree cover exceeded 40% the potential increase was as low as 5%. Frost, a-pan evaporation and growing season length were not significant explanatory co-variables and were removed from the analysis based on the best model fit (Table 3).

Table 4: Best fit ANCOVA model investigating the drivers of landuse driving woody cover change

Model ***Variables in bold are significant***	**AIC value**
% Woody cover change **~ Land use** + **Rainfall group** + **Starting cover** + No. Frost days + Apan evaporation + **Mean annual temperature**	390.9
% Woody cover change **~ Land use** + **Rainfall group** + **Starting cover** + Apan evaporation + **Mean annual temperature**	388,93
% Woody cover change **~ Land use** + **Rainfall group** + **Starting cover** + **Mean annual temperature**	**387.33**

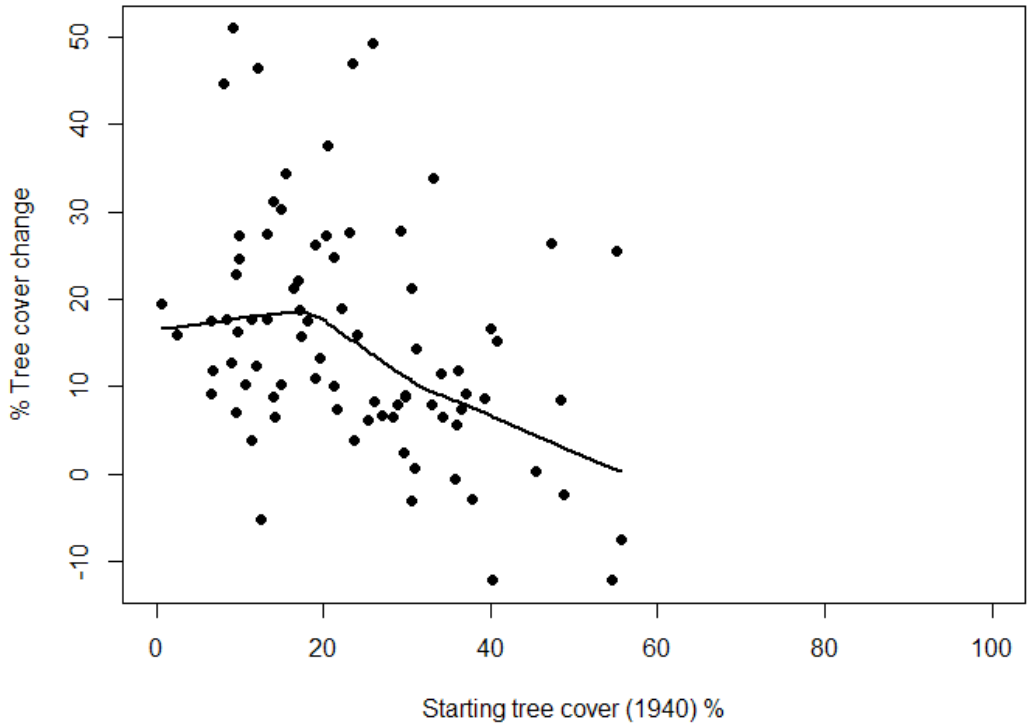

Figure 5: Scatterplot of starting tree cover (1940) plotted against total tree cover change (%), with a lowess smoother fitted (solid line). Tree cover increases were highest when starting tree cover was low (<20%). When starting tree cover exceeded 20%, the tree cover change potential declined. When starting tree cover exceeds 40% the potential for encroachment to occur is almost zero.

A plot of percent woody cover change for each site against mean annual rainfall (Figure 6) shows that almost all sites had experienced increased tree cover, as the majority of the points, regardless of landuse had positive Y values. A smoothed lowess fit indicates that when MAP > 600 mm tree cover increases became larger. (Figure 6). As rainfall increased, there was an increase in the number of sites exceeding 40% woody coverage (Figure 7), a critical threshold where grass production begins to decline. In 1940 only 31% of all the sites exceeded 40% cover, but in 2009, 72% of sites exceeded 40% woody cover showing an increase in the number of areas that are vulnerable to biome shifts.

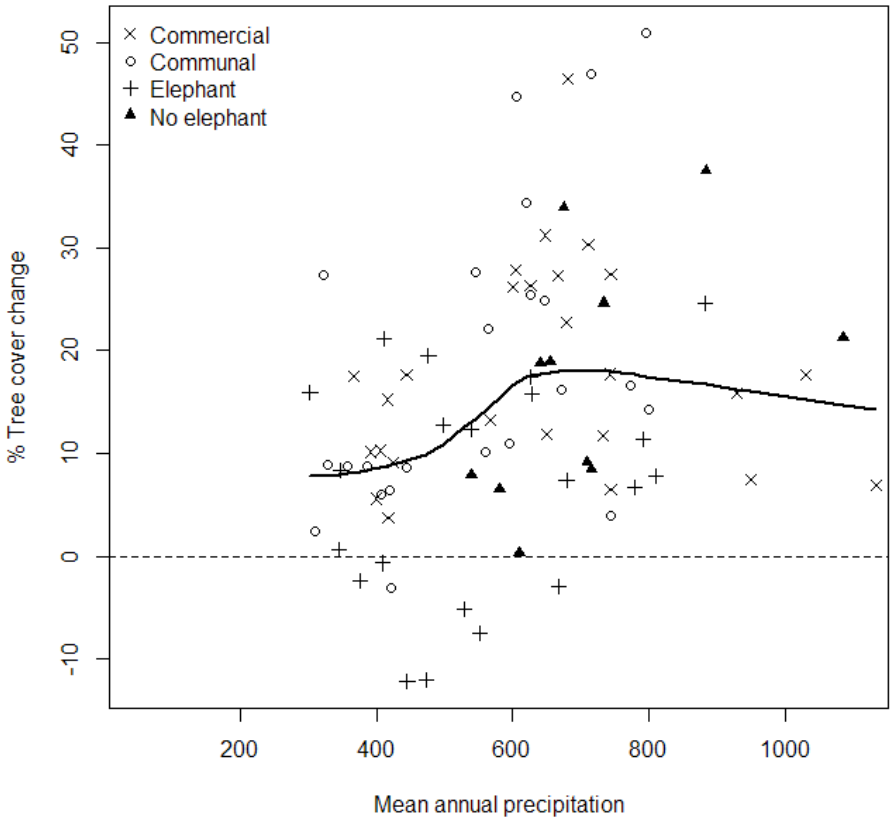

Figure 6: Scatterplot of percentage tree cover change over time against mean annual precipitation. The different landuses are represented by different symbols. Change occurs across all landuses. Tree cover increases increased with increasing rainfall, when MAP > 600mm, increases in treecover changes were greatest, thereafter stabilising and eventually tailing off at the highest rainfalls.

CO_2 fertilisation in arid savannas

A comparison of tree cover site pairs (1940 v. 2009) against the established relationship for maximim woody cover and mean annual rainfall for African savannas (Equation: Cover (%) = 0.14(MAP) - 14.2, between 101mm – 674mm) (Figure 7) showed that 6 % of the site pairs exceeded the maximum tree cover threshold in both 1940 and 2009. However, by 2009 20% of the sites in the low rainfall areas exceeded the maximum tree cover threshold calculated for African savannas (Sankaran 2005). In terms of area, 11% of the measured area exceeded the maximum tree cover threshold.

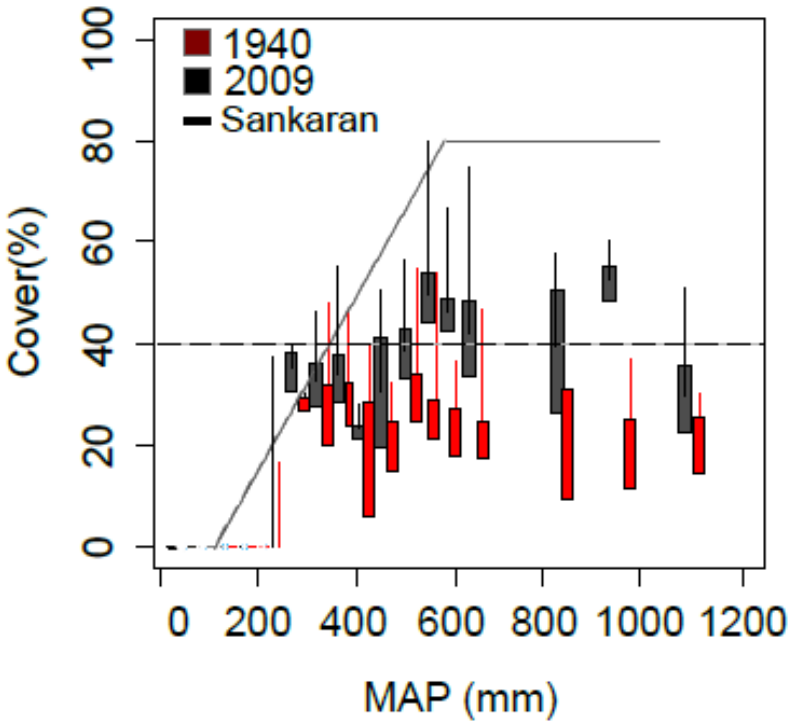

Figure 7: Tree cover (in 50mm bins) against mean annual rainfall for 1940 (black) and 2009 (red). The box center represents the mean, the box represents the standard error and the lines represent the 0.99 quantile for the 50mm classes. The solid black line represents the maximum tree cover vs MAP relationship for African savannas and is represented by the equation: Cover(%) = 0.14(MAP) - 14.2. between 101 - 650 mm of MAP. Dashed lines represents the 40% tree cover threshold.

Discussion

We present the first regional scale long-term analysis of woody cover change in South African savannas. Widespread increases in woody cover have occurred across South African savannas since the 1940's, regardless of landuse. The sole exception was for conservation areas in arid regions when elephants were present. Maximum tree cover potential in arid savannas has increased from the 1940's to 2009. Tree cover in 20% of arid savanna sites had exceeded the maximum tree cover threshold calculated for African savannas (Sankaran et al, 2005) in 2009, whereas only 6% of the sites exceeded this threshold in the 1940s.

The role of local drivers on tree cover change

Our results are consistent with those of Wigley et al. (2010), and demonstrate that widespread tree cover increases have occurred irrespective of land use, strongly indicating that a global driver is causing woody increases. The low tree cover "increase potential" with higher starting tree cover may indicate that this process is bounded. However when tree cover exceeds 40%, grass production will decline increasing the likelihood of fire being excluded creating the potential for a biome switch (Scholes, 2003; Archibald et al, 2009; Bond & Midgley, 2012). Although local landuse is undoubtedly an important driver in tree cover changes (Todd & Hoffmann 2007; Fynn & O'Connor 2000), our results show that the influence of local drivers have been swamped by a regional or global driver. It was expected that the four selected land uses, each characterized by very different land management strategies, would produce different trajectories of tree cover change over time. Instead all tree cover classes experienced a significant increase. Large increases in tree cover were expected in the commercial rangelands as they are grazer dominated systems with low fire return intervals, both of which are expected to promote tree growth and establishment due to the low grass cover (Roques et al. 2001; February et al, 2013; Riginos &Young, 2007) and long fire free intervals (Smit et al, 2010) facilitating escape from the fire trap (Higgins et al, 2000). However decreases in woody cover are widely predicted for communal rangelands (Banks et al, 1996; Matsika et al, 2013; Wessels et al, 2013), primarily due to the high human population densities (www.census2011.co.za) (Table 1), leading to heavy utilization of the woody resources for fuel and building (Banks et al, 1996). Consequently these areas were expected to have fewer trees, lower woody cover and lower levels of regeneration capacity than the other land uses (Bucini & Hanan, 2007, Higgins et al, 1999). Tree demography surveys (Wessels *et al*, 2011) in these areas indicate that a large proportion of the woody cover is from shrubs, less than 3m in height. Frequently shrubs are the dominant woody form responsible for encroachment (Skarpe 1990; Buitenwerf et al, 2011, Knapp et al, 2007), and are likely to be so in communal rangelands. A possible explanation for the increase in shrubs is facilitation of clonal spread by root suckering with increased carbon gain under increasing atmospheric CO_2 (Wakeling & Bond, 2007; Bond & Midgley, 2012)

Conservation areas in Africa represent a unique 'control' for global change studies since they retain the indigenous megafauna, have low human impacts, and generally burnt on a regular basis. They are characterized by a near continuous land use history where a complete suite of ecological processes (frequent fires, grazer and browser presence) have been maintained. If

land use is driving woody thickening, then tree cover should decrease or at least remain stable over time. A high fire frequency (Smit et al, 2010) with a moderate grazing pressure does not favour increases in tree cover (Asner et al, 2009), while the browsers have a clear negative relationship with woody cover (Sankaran et al, 2008) as they can suppress growth, maintain woody vegetation within the flame zone and can prevent seedling establishment (Bucini & Hanan 2007, Prins & van der Jeugd 1993; Staver et al. 2009). The presence of elephant in conservation areas should decrease tree cover and biomass (Asner et al, 2009; Dublin et al, 1990; De Beer et al, 2006). Our results however demonstrated that this was only true for the low rainfall areas. The varying response with rainfall can be explained by a hypothesis that suggests that the direct effects of herbivory are modulated by ecosystem productivity (Skarpe, 1992; Pringle et al, 2007). Large herbivores are strong "interactors" when the productivity (e.g. rainfall) is low, potentially due to faster compensatory growth in more productive systems causing herbivores to have a lower net impact of plant biomass in more mesic areas. Therefore actions such as the loss and exclusion of large herbivores in arid areas are predicted to have profound impacts (Pringle et al. 2007). The large increases in cover in the mesic conservation areas, did not, however, meet our expectations of zero or little change.

Global drivers and the increase of tree cover

Maximum tree cover potential and the realized woody cover in semiarid African savannas is strongly limited by mean annual precipitation (Sankaran et al. 2005). Tree cover in mesic savannas, however is disturbance limited (Sankaran et al, 2005). Rainfall characteristics such as rainfall intensity and storm depth can therefore influence woody cover changes, particularly in the low rainfall areas (Good & Caylor; 2011). Therefore increases in either rainfall intensity or mean annual precipitation should increase regional woody cover in these areas (Sankaran et al, 2005; Sankaran et al, 2008; Bucini & Hanan, 2007; Goods & Caylor, 2011; Kulmatski & Beard, 2013). Although our results showed widespread increases in tree cover, they did not show a disproportionately high increase in tree cover in the low rainfall areas; rather, larger increases were restricted to the higher rainfall areas. Analysis of the climate records for the savanna regions of South Africa show increases in precipitation intensity in the high rainfall savannas (Kruger, 2006). However the low rainfall savanna regions have experienced shorter annual wet spells and a decrease in precipitation intensity (Mason et al 1996; Kruger, 2006). Additionally mean annual precipitation at sites specifically in Northern Limpopo and Mpumalanga have experienced significant decreases in long-term annual precipitation (Mason et al, 1996; Kruger, 2006), with rain stations in the lowveld (the

heart of SA semiarid savannas) experiencing a 38% decrease in annual rainfall totals since 1931 (Mason et al 1996). The patterns of observed tree cover increase cannot be explained by decreasing mean annual rainfall and precipitation intensity, which should result in the opposite trend and drive a net decrease in tree cover.

Of the regional drivers CO_2 fertilization driven by elevated atmospheric CO_2 levels best explains our results. Our results are consistent with existing predictions (Bond & Midgley, 2000), models (Higgins & Scheiter, 2012) and field studies (Wigley et al. 2010, Buitenwerf et al, 2012) all of which indicate that increasing CO_2 concentrations will increase woody plant biomass and dominance. The increases in high rainfall savannas, where fires are frequent, can best be explained by an increased probability of sapling escape from the fire trap (Hoffmann et al, 2000; Bond & Midgley, 2000; Kgope et al, 2010; Bond & Midgley, 2012) achieved by greater below ground storage reserves (Kgope et al, 2010; Bond & Midgley, 2012). Increases in tree cover in arid systems are best explained by the indirect effect of increasing soil moisture, driven by improved water use efficiencies (Polley et al, 1997). It is predicted, here, that any rise in CO_2 will produce an increase in the available soil moisture and thus increase the maximum tree cover potential. Using this principle, Donohue et al (2013) demonstrated that elevated CO_2 most likely accounted for an 11% increase in annual maximum greening in semi-arid areas worldwide. Likewise we demonstrated that not only did tree cover increase across all land uses in the arid sites but tree cover in 2009 frequently exceeded the upper tree cover bound for African savannas (Sankaran et al, 2005). This result is especially relevant since during this period decreases in mean annual precipitation and rainfall intensity have occurred in these areas, Our results are also important in indicating woody increase in the lower rainfall areas. Bond & Midgley, (2012) suggested that, based on the existing evidence, woody increase was most prominent in mesic savannas. A study on tree and shrub cover changes in the 50 year burning experiments in Kruger National Park which showed negligible changes in a semi-arid savanna but five to ten-fold increases in woody plant density in a mesic savanna (Buitenwerf et al, 2012). However our study, over a much larger region, shows that general woody increases are also occurring in the drier savannas though the magnitude of changes is not as great as in their high rainfall counterparts.

Consequences of widespread tree cover increases

Our results indicate widespread tree cover increases have occurred across South African savannas, and a large shift from open systems to increasingly closed systems is occurring. We also noted that in the 2009 sites, tree cover in many areas had exceeded 40%, the threshold where grass production and hence fire frequency rapidly declines. Using our results we cannot determine if these areas have undergone a biome shift to closed woody systems accompanied by altered species composition. However they certainly do highlight that a large proportion of the landscape, especially in the high rainfall areas, is vulnerable to potential biome shifts and a dramatic alteration of ecosystem function e.g. reduction of fire (Archibald et al, 2009).

Such an increase in tree cover in savannas has costly economic (Mugasi et al, 2009) and ecological consequences (Blaum et al, 2007; Sirami et al, 2009. Ecosystems services, e.g. water supply and nutrient cycling, will be altered (Asner et al, 2004) and biodiversity losses will occur (Blaum et al, 2007, Sirami et al, 2009, Rajajczak et al, 2012). Stocking rates are expected to drop, tourism potential for conservation area may decline (Gray & Bond, 2013) and the costs of woody plant clearing will increase. The widespread woody increases within our study site indicate these changes will affect most land users. This should highlight the need for a review of existing land management policies, and the formulation of novel strategies to manage this problem. As encroachment probably occurs gradually, the extent of the problem up until now has been underestimated. An assessment of the ecological and economic costs of bush encroachment should be made at a national level to bring attention to this impact and to highlight the costs of this change. Overall this study highlights the need to initiate and hasten the development of a national management strategy to address this problem.

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Chapter 3: Investigating potential determinants of the distribution limits of a savanna woody plant; *Colophospermum mopane*

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NS designed the experiment, collected data, performed the analysis and wrote the manuscript. LE assisted withfield data collectionand commented on the manuscript, BE is a supervisor and commented on the manuscript. AS provided access to facilities and funded the field component of the work

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Abstract

Questions

Early bioclimatic models predict that climate change in southern African savannas will cause a huge southward and westward range shift of the savanna tree *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J.Léon. *C. mopane* is an economically and ecologically important subtropical savanna tree that forms mono-dominant stands across 25% of southern African savannas. We investigate the validity of these initial range expansion predictions using a regional-scale, climate envelope niche model, and fine-scale field mapping of the current boundary, to understand; What are the regional scale drivers of the distribution of *Colophospermum mopane* in southern African savannas? What are the landscape scale distribution patterns of this species?

Location

Central Lowveld, Kruger National Park, South Africa

Methods

We investigate the validity of very early range expansion modelling predictions using a regional-scale, climate envelope niche model, and fine-scale field mapping of the current boundary, to understand which environmental variables may determine the distribution limit of this signature species

Results

Our findings indicate that both non-climatic (dry season day length) and climatic (minimum temperatures) variables limit the regional distribution of *C. mopane*. At the landscape scale, the distribution of this species is restricted to the warmer parts of the landscape, suggesting minimum temperature appears to be the primary factor determining its landscape-scale distribution

Conclusions

This study provides the first detailed model of the environmental factors that may limit the regional distribution of *C. mopane* and allows us to formulate testable hypotheses regarding the determinants of the range of a keystone species.

Keywords: species distribution modeling; savanna; South Africa; MAXENT; mopane; range limits, Kruger National Park, climate change

Introduction

The global distribution of plants is frequently attributed to climate, as it reflects the availability of moisture and energy for plant growth (Polis 1999, Gaston 2003, McInnes et al. 2009). This general understanding is often assumed to extend to plant communities occurring in subtropical savanna regions of the world, particularly at regional and continental scales. Recent research, however, indicates that non-climatic environmental factors (e.g. day length, fire and competition), can also significantly affect the distribution of plant communities at both regional and landscape scales (Chuine & Beaubien 2001, Bond et al. 2005, Gaston 2009, Staver et al. 2011). We therefore investigated the regional determinants and landscape distribution patterns of an economically and ecologically important subtropical tree *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J.Léon, that occurs in semi-arid savannas of South Africa. We aim to understand the determinants in driving this keystone species range limits as a necessary first step in improving the predictive understanding of this important species' response to global climatic change.

Colophospermum mopane is a dominant leguminous tree or multi-stemmed shrub, belonging to the Caesalpinoideae sub-family, which occurs in hot, low-lying regions of subtropical southern Africa. It is estimated to dominate, often in monospecific stands, 20-25 % of the 1.5 million km^2 (White 1983) of savanna in southern Africa (Mapaure 1994, Timberlake 1995), resulting in extensive areas with a low compositional and structural diversity. Importantly, this species has been predicted to extend southwards and westwards of its current distribution (Rutherford et al. 1999). Such a range shift could have extensive ecological and economic impacts (both positive and negative) given its tendency to form mono-specific stands. Despite its great ecological significance, the underlying factors controlling *C. mopane* distribution limits are not well established.

Early studies suggest that *C. mopane* does not occur where the average July temperature is below 5 ^{o}C (Henning & White 1974). Additionally, seedling survival is critically limited by soil moisture availability (Harrington 1991, Stevens *unpublished data*) and mediated by shade and competition with grass (Mlambo & Nyathi 2001, Mlambo 2007, van der Waal et al. 2009). Increased precipitation can enhance *C. mopane* seedling establishment success; alternatively it may reduce the likelihood of *C. mopane* persistence

through increasing competition from higher grass production and an associated increased fire frequency (Archibald et al. 2009). Recent work on savanna tree growth has also demonstrated that day length shortening during the dry season causes a cessation of above-ground growth, independent of temperature, thus implying that dry season day length may be an important additional component in determining southern distribution limits of subtropical tree species (Wakeling et al. 2012).

Although all of these aspects may be important determinants of *C. mopane* distribution, there is little evidence showing which factors, or combinations thereof, determine the southern distribution limit of this species. To address this knowledge gap we investigated the validity of the initial predictions of range expansion of *C. mopane* (Rutherford et al. 1999), using a regional-scale maximum entropy (MAXENT v 3.3.3a) model (Phillips et al. 2006) to ascertain which key climatic and non-climatic variables are important determinants of the distribution limits of this species. The model was built using environmental metrics relating to four principal variables that have been hypothesised to limit the distribution of *C. mopane*: temperature, precipitation, day length, and fire frequency (Table 1). The limiting factors functionality in MAXENT 3.3.3a (Elith et al. 2010) was used to demonstrate which environmental variables most influence the predicted *C. mopane* distribution across its range. We compared these modeled regional findings for the lowveld of South Africa and compared them to distribution patterns observed at the landscape scale, where we mapped *C. mopane* distribution patterns in the field at sites at the edge and away from the edge of the southern distribution limit. Differences in landscape scale distribution patterns between these sites were used to infer the importance of temperature in controlling the current local distribution.

Methods

Regional distribution determinants

Species records

Ninety three distribution records of *C. mopane* within southern Africa were extracted from the online database of the South African Biodiversity Information Facility (http://sibis.sanbi.org). The points originated from PRECIS (National Herbarium Pretoria (**PRE**) **C**omputerised **I**nformation **S**ystem). PRECIS is an electronic database system on southern African plants. The locations come from the southern African collection held in the

National Herbarium, Pretoria and the collections of the Compton Herbarium and the South African Museum. The localities of the points are distinguished using a quarter degree grid reference (~25 km x 25 km) or global positioning system co-ordinates. To demonstrate the presence of *C. mopane*, a centroid from a quarter degree grid was taken. In so doing, we converted the presence of *C. mopane* within a 25 km x 25 km grid, to a point. However as all the environmental data was resampled to a resolution of 18.5 km x 18.5 km, the presence of a point in one pixel now represented the presence within 18.5 km x 18.5 km, thus ensuring that little information about the distribution of *C. mopane* was lost through this conversion.

Environmental data

We selected southern Africa (south of 10°S latitude) for the model of *C.mopane* distribution. We acknowledge that the selection of model area extent and the associated training area may have an influence on model output (Barve et al. 2011). In the absence of data on the palaeo-distribution of *C. mopane*, as suggested by Barve et al. (2011), we have to rely on more general estimates of conditions conducive to the development of savanna elements (Scheiter et al. 2012). The numerous temperature and precipitation variables, covering the extent of southern Africa, were extracted from the WORLDCLIM database (version 1.4, http://www.worldclim.org) which were created from the interpolation of weather station records from 1950-2000 at a spatial resolution of 30 arc-second grid (18.5 km x 18.5 km) (Hijmans et al. 2005). A fire frequency layer (resolution 500 m^2) was created from eight years of burnt area data from the MODIS (MCD45A1) product (Roy et al. 2008, Archibald et al. 2010). We created a day length layer by generating a matrix of daily day length across 0.15 x 0.15 decimal degree grids. This was calculated in R (R Development Core team 2010) using the following formulae:

Day Length = 24 / pi * Sun Angle (1)

Sun Angle = acos (-tan (Latitude) * tan (Declination)) (2)

Declination = 0.409 * sin (Julian Day - 1.39) (3)

Julian Day = (2 * pi / 365) * Day of Year (4)

The mean monthly daylight hours were averaged to represent average daylight hours in the growing season (October – March) and dry season (April – September).

As co-linearity is probable in climatic data and can cause model over-fitting we performed pair-wise Pearson's correlations between all the spatial layers of interest. Layers were excluded from further analysis if the correlation was greater than 0.85 (Table 1, for list of all variables included in the model) (Elith et al. 2006). All environmental layers were edited in ArcGIS 9.3 (ESRI, 2006) to ensure identical projections, grid cell size and alignment, and spatial extent across all layers. All environmental layers were resampled to the coarsest resolution (thus matching the WORLDCLIM environmental layers).

Distribution modelling

To model the geographical distribution of *C. mopane*, we used MAXENT version 3.3.3 a (Phillips et al. 2006, Elith et al. 2010). MAXENT was selected as it is a freely available, general-purpose method for making species distribution predictions from presence only data (Phillips *et al.* 2006). Evaluations of its performance indicate that it is robust and consistently competitive with other modelling methods (Elith et al. 2006, Elith et al. 2010). MAXENT evaluates the suitability of each grid cell as a function of the environmental variables within that cell by comparing the species presence data with the background data (10,000 random points) (Phillips et al. 2006) (MAXENT software and further information on this method are available from http://www.cs.princeton.edu/~schapire/maxent). Models were built using 75% of the data with the remaining 25% used as a test sample. A jack-knife method was used to measure individual variable importance in model development, and receiver operating characteristic analysis (ROC) was used to assess model quality (Fielding & Bell 1997). A ROC plot was built by plotting the sensitivity values and the false positive fraction for all available probability thresholds (Manel et al. 2001). The area under the curve (AUC) test statistic measures the area under the ROC curve, and the values range from 0.5 to 1.0. A value of 0.5 suggests the model fit is no better than random, while values higher than 0.8 indicate a good model fit (Fielding & Bell 1997, Phillips et al. 2006). We also applied the limiting factors function, which demonstrates spatially, on a pixel by pixel basis, which environmental variable most influences the prediction for the given cell, and is therefore the most limiting variable in each predicted grid cell (Elith et al. 2010).

Landscape distribution determinants

Study area

To improve our understanding on how effective the model is, we focused on the lowveld region of *C. mopane* distribution and investigated how the landscape distribution patterns matched predictions specific to this broader region. The area in which we focused is the block of *C. mopane* that runs south from the eastern part of the Soutpansberg to the Olifants River. We refer to this region the lowveld, following the convention in southern Africa of using this term for low altitude areas (~300 m – 500 m) of Mpumalanga and Limpopo provinces. To investigate the landscape distribution patterns of *C. mopane*, two study sites were mapped: 1) a non-edge site (~ 31°13′15E, 28°54′41S), 50 km north of the *C. mopane* southern distribution limit, situated in the Phalaborwa section of the Kruger National Park (KNP); and 2) an edge site (~ 31°23′12E, 24°22′3S), situated at the edge of the species' southern distribution limit, in the Kingfisherspruit section of the KNP (Fig. 1). Three catenal slopes were mapped at both the non-edge sites and edge sites respectively. Both sites have similar mean annual rainfall, geology, and elevation ranges. The climate of both sites is characterized by hot, wet summers and mild, dry winters. The non-edge and edge sites have a mean annual temperature of 22.4 °C and 23.1 °C respectively. The mean annual rainfall at the non-edge site is 481 mm (South African Weather Service, Phalaborwa station) and at the edge site is 532 mm (LEDET 2008). The elevation range at the non-edge site is 350-500 ma.sl. and the edge site is 370-470 ma.sl. Both sites are underlain by granite/gneiss parent material and the landscapes consist of moderately undulating hills (Gertenbach 1983, Venter et al. 2003) with a distinct granitic catenal sequence: sandy soils on the crests and clayey soils along the footslopes (Scholes & Walker 1993, Venter et al. 2003). Woody vegetation at both sites is dominated by *C. mopane* interspersed with *Combretum apiculatum* (Gertenbach 1983).

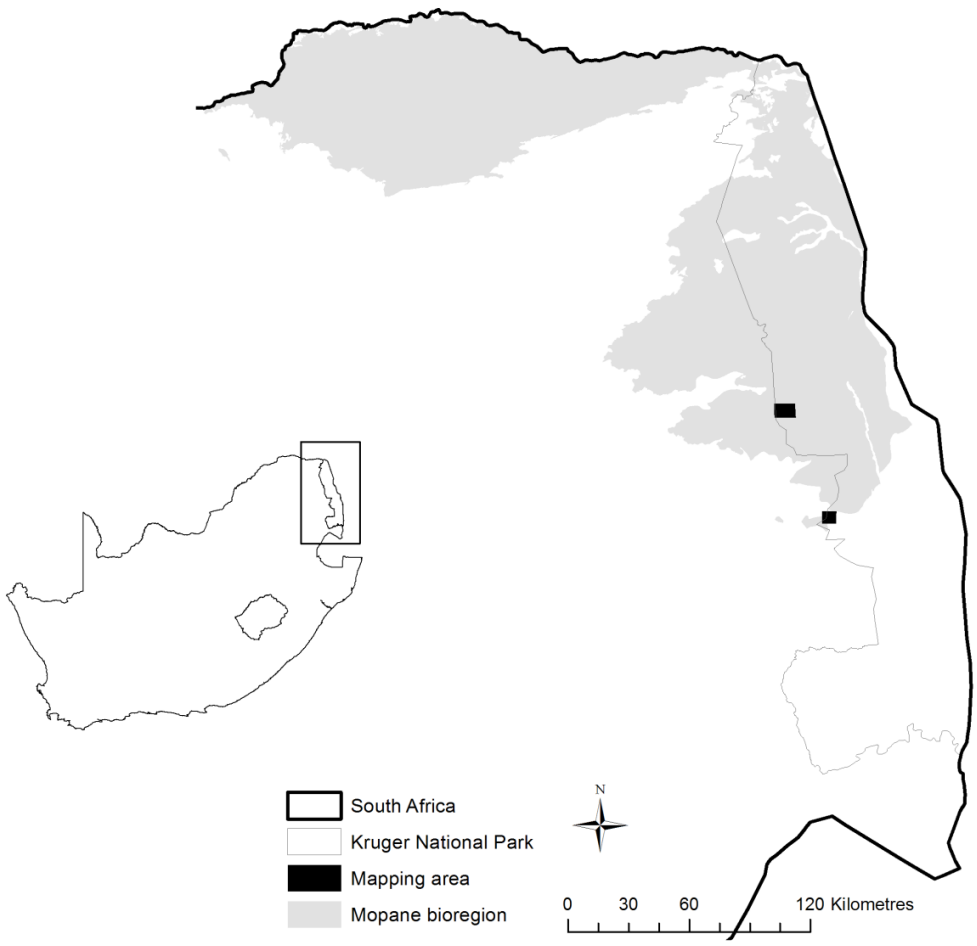

Figure 2.1:*C. mopane* distribution in South Africa (Mucina & Rutherford 2006). Field study sites are located at and away from the *C. mopane* range edge.

Field Mapping

Surveys were conducted in May and June of 2008 and 2009. Two teams of observers, using Cybertracker software (http://www.cybertracker.org) on Fujitsu Siemens Loox N520 Pocket PC's, walked 40 m wide belt transects on due north/south bearings (perpendicular to the species boundary), using roads that surrounded the sites to designate the area to be mapped. Observers walked down the centre of the transect and recorded the presence of all *C. mopane* trees, 20 m on either side of the transect. If there were more than five individual *C. mopane* trees occurring within a 20 m radius the area was defined as a "patch" and was mapped accordingly. When the start of a *C. mopane* patch occurred, the geographical coordinates were recorded and the start patch was manually recorded as a "start patch edge". When the

end of the patch edge was reached, a geographical co-ordinate was taken and manually recorded as "end patch edge". In addition, the Cybertracker software automatically logged the observer's location and elevation every 15-30 seconds. We used the manually recorded start and end patch locations to classify the automatically logged locations as "mopane patch", or "no mopane". All subsequent analysis was conducted on these automatically logged locations. Single *C. mopane* trees, not occurring in a patch were recorded as "lone trees". A total transect length of 350 km was surveyed at each site.

Landscape distribution patterns

All geographical coordinates were viewed in ARCMAP 9.3. Automatically recorded geographical coordinates were assigned a presence or absence value, based on the delineation assigned by the manually recorded patch edge locations. A presence value was assigned for each coordinate recorded between a "start patch" and "end patch" record, within a transect. Points indicating a patch on adjacent transects were joined up in ARCMAP 9.3, to create a two-dimensional map of patches across the full extent of each study site. This allowed for a comparison of patch structure between sites. To compare the distribution of *C. mopane* along the catenas of the edge and non-edge sites we rescaled the location of the presence points for every catena, relative to the lowest and highest elevation points. We calculated the altitude of every point as a percentage, relative to the entire altitudinal range of each catena, using the following formula:

(Elevation at point – Lowest point across catena)/ (Highest point across catena – Lowest point across catena) *100 (5)

We then divided the relative altitude along the catena's into 5 % bands and calculated the number of *C. mopane* presence points in each elevation band. The total number of presence points was then summed for each site, and a measure of *C. mopane* abundance was calculated as:

(Number of *C. mopane* presence points in each elevation band)/ (Total number of *C. mopane* present in the site) * 100 (6)

We used a Kolmogorov–Smirnov test in R version 2.14.0 (R Development Core team 2012) test to determine if the *C. mopane* frequency distribution along the catena differed between the edge and non-edge populations. We used FRAGSTATS version 3.3 (McGarigal & Marks 1995) to quantify three landscape metrics to compare the patch structure in the non-edge

(northern) and edge (southern sites). We examined the largest patch index (LPI) which measures the percentage of the total landscape area that is comprised of the single largest patch. The LPI ranges between 0-100, if the LPI = 100 the entire landscape consists of a single patch. The landscape shape index (LSI) is a standardized measure of total edge that adjusts for the size of the landscape. If the LSI=1, the landscape consists of a single square patch. The LSI increases as patches become more irregular and the lengths of their edges increases. Contagion (CONTIG) is a measure of the aggregation and interspersion of patches across a landscape. It is a percentage and ranges between 0 – 100. When CONTIG = 100 the landscape consists of a single patch. As CONTIG approaches 0 the patches are maximally interspersed.

Results

Regional distribution determinants

The variables in the MAXENT model produced a good fit as the AUC value for the training data was 0.933 and the AUC value for the test data was 0.90. The jacknife test revealed that the environmental variable with highest gain when used in isolation was average day length during the dry season, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is minimum temperature in the coldest month, which therefore appears to have the most information that is not present in the other variables. Overall, at the regional scale, average dry season day length and minimum temperature in the coldest month were the strongest determinants of the distribution of *C. mopane*, accounting for 42.2% and 26.4% respectively of the modelled distribution (Table 1). The model indicated that the probability of *C. mopane* presence drops below 50% as minimum temperatures decrease below 4.8 °C in the coldest month (July), and the average number of dry season daylight hours drops below 11 h 3 mins. Precipitation in the wettest quarter contributed to 23.5% of the variance in the modelled *C. mopane* distribution, where the probability of *C. mopane* presence drops below 50% when precipitation exceeds 380 mm in the wettest quarter. Precipitation in the driest quarter and fire frequency were not important in determining the distribution of *C. mopane*.

Table 2.1: Contribution of environmental variables included in the MAXENT model

Variable	Source	Variable importance (% contribution to model)
Average dry season day length	Equation [1]	42.2
Minimum temperature in coldest month	WORLDCLIM	26.4
Precipitation in wettest quarter	WORLDCLIM	23.5
Precipitation in driest quarter	WORLDCLIM	4.1
Fire frequency	MODIS	3.7

Table 2.2: Description of landscape metrics used to describe the patches of *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J (McGarigal & Marks 1995). Non-edge patches occurred 50km north of the distribution limit of *C. mopane*, edge patches occurred at the southern distribution limit of *C.mopane.*

Landscape metrics	Non-edge	Edge
Largest patch index (LPI)	85.4 %	36.4 %
Landscape shape index (LSI)	4.05	6.4
Contagion (CONTIG)	94 %	69 %

Under current climate conditions, the bulk of *C. mopane* distribution was predicted to occur slightly north of the Tropic of Capricorn (extending north of the Soutpansburg into the Limpopo Valley) (Fig. 2) with a southwards extension of *C. mopane* range, east of the Soutpansberg mountains into low-lying eastern South Africa, where it meets its southern-most distribution limit. The map of limiting factors demonstrates that four environmental variables can be important in limiting the modelled distribution of *C. mopane* across southern Africa (Fig. 3). Minimum temperature is predicted to limit the northern distribution band (north of the Soutpansberg, in the Limpopo valley) from entering the cold interior of the southern African Highveld, and may limit the western spread of *C. mopane* from its current distribution range within the mapping study region, in the South African lowveld, where minimum temperatures drop below 4.8 °C at the eastern escarpment. The limiting factors

model predicted that northward expansion of *C. mopane* is limited when precipitation in the wettest quarter exceeds 380 mm, while less than 50 mm rainfall in the wettest quarter prevents *C. mopane* expansion into the south-western edge of its range. Dry season day length is an important variable limiting *C. mopane* from occurring further south in the warm, semi-arid South African lowveld.

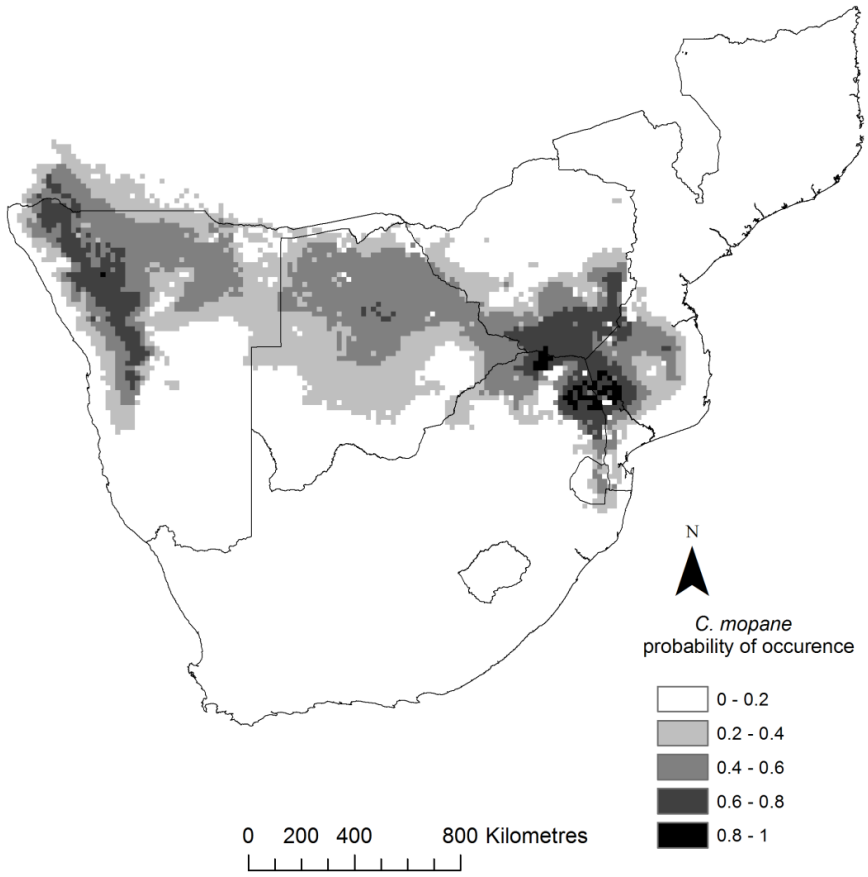

Figure 2: Modelled distribution of *C. mopane* based on 4 environmental variables (average dry season day length, minimum temperature in coldest month, precipitation in wettest quarter, precipitation in driest quarter, and fire frequency) using a maximum entropy model, MAXENT.

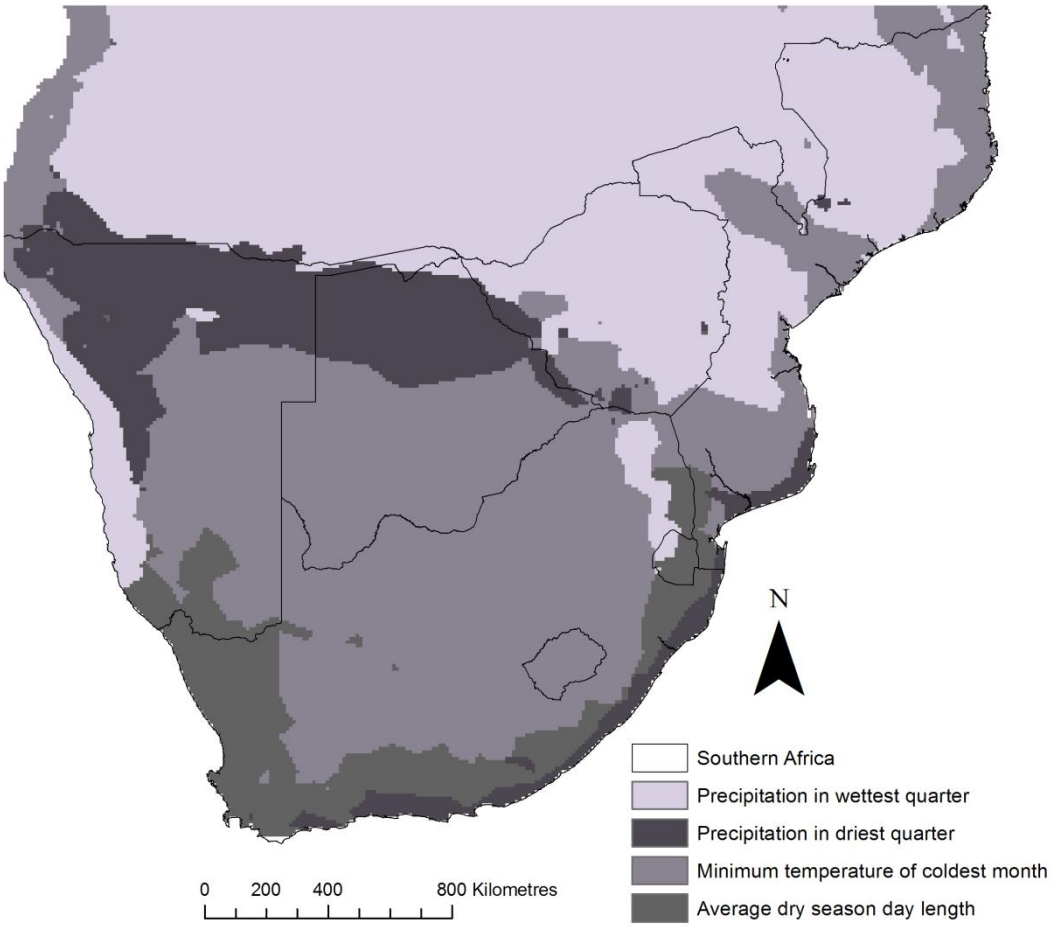

Figure 3: A map of southern Africa displaying which environmental variables are most likely to limit the current distribution of *C. mopane*, as predicted by our MAXENT model. The most limiting factor is the variable that influences the model prediction the most in a grid cell.

Landscape distribution patterns

A total of 22 000 observation points over 600 km of transect revealed significant differences in the distribution patterns of *C. mopane* across catenal slopes between non-edge and edge populations (Fig. 4). Stands of *C. mopane* at the edge site show a significantly different distribution across the catenal slope compared to populations occurring in the non-edge areas (Kolmorogov-Smirnov test; D= 0.5, p =0.014). At the edge site, *C. mopane* occurred predominantly (97%) on the upper mid-slope position in the landscape (Fig. 4). The non-edge populations showed a dispersed distribution, with only 64% of *C. mopane* observations

occurring on the upper mid-slopes. *C. mopane* was all but absent from the ridge crests at both sites.

Patch distribution and pattern were strongly affected by latitude as the distribution of *C. mopane* in the northern non-edge sites differed markedly from the distribution of *C. mopane* at the southern edge sites (Table 2). Patches at the edge sites were on average 50 % smaller, were more numerous and had lower CONTIG (Table 2) values, indicating they were spatially more dispersed than their northern counterparts. Non-edge patches were very large and continuous. LSI (Table 2) values indicated that patches were also more irregularly shaped at the edge of the distribution range.

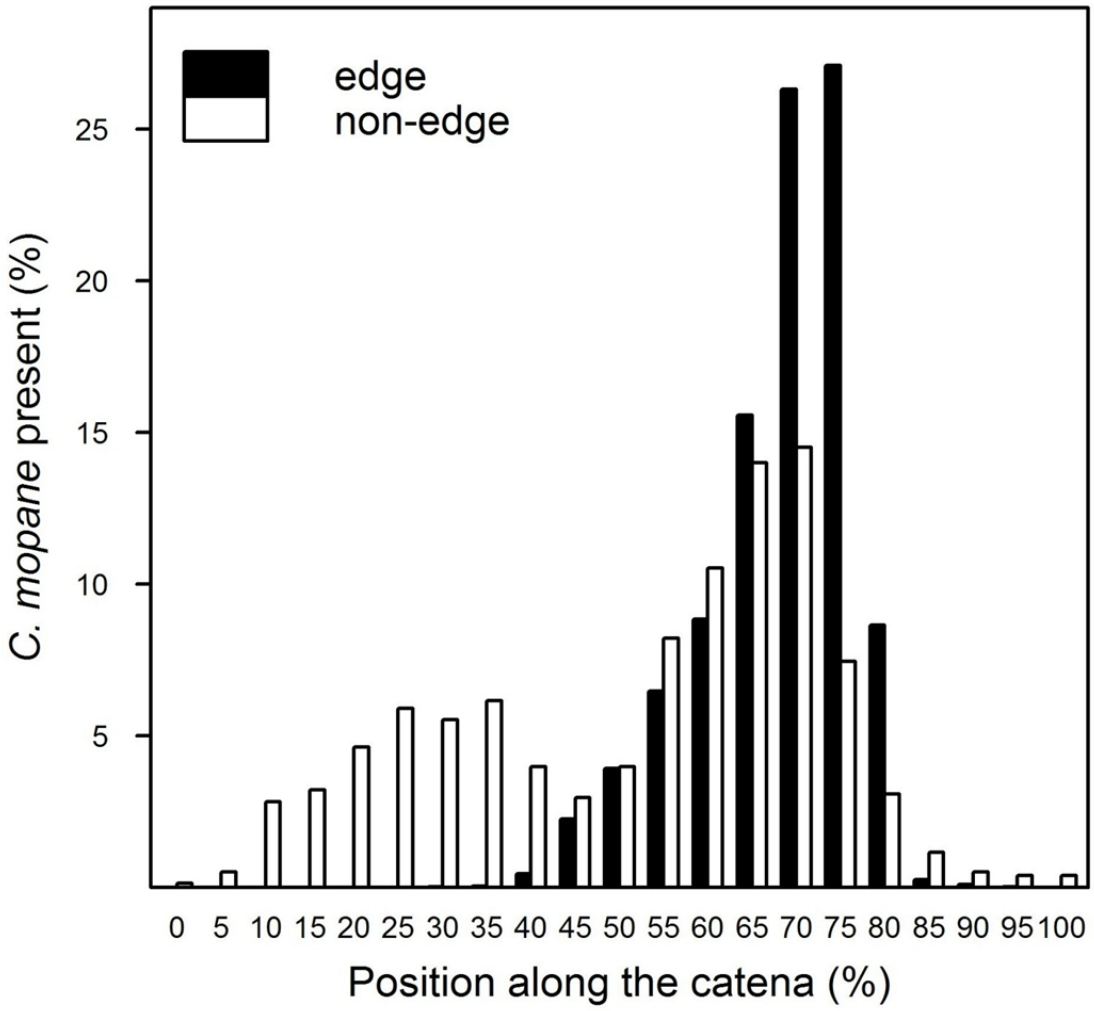

Figure 4: A histogram showing the frequency of sampling points at which *C. mopane* was present along hill slopes at the edge of the distribution (South) and away from the edge (North). Unlike at the

non-edge site, *C. mopane* is absent from the lower slopes at the edge site (Kolmogorov-Smirnov test D= 0.5, p =0.014*).

Discussion

Regional distribution limits

Our MAXENT analysis showed that the predicted regional-scale distribution of *C. mopane* is not likely to be controlled by climatic variables alone.

Of the climatic controls included, minimum temperature was a primary factor in limiting the distribution in the central interior of southern Africa, whilst dry season day length, a non-climatic variable, was a key factor that explained most of the distribution at its southern edge in the eastern lowveld of South Africa. This is an important finding as we confirm that drivers of landscape patterns are not always uniform across space (Peters et al. 2006). This consideration is frequently overlooked in species distribution models, which fail to acknowledge that many systems are heterogeneous in space and time (Wu & Loucks 1995). It has been highlighted that the determinants of ranges differ between the pole and equatorial edges (Normand et al. 2009) but it is seldom shown that individual limiting variables vary along the same edge. We demonstrate that this is an important component in understanding range edges and it should be explicitly considered when providing recommendations and predictions as to the extent of species range shifts. The findings from our study indicate that the response of *C. mopane* to climate change will differ from that predicted by Rutherford et al. (1999). Although we do not explore model- and predictor variable related difference in this paper, there has been significant technical improvements in modelling methods and the collation of regional climate surfaces (Hijmans et al. 2005) since Rutherford et al.'s (1999) bioclimatic envelope model. Rutherford et al. (1999) use only climatic variables to explain distributions, whilst our model suggests that climatic factors interact with day length to potentially limit the future spread of *C. mopane.* Rutherford et al.'s (1999) method did not have a mechanism to investigate the effects of different limiting factors at different range edges, and this, together with the absence of non-climatic factors, is likely to account for the difference with our findings.

The role of day length, and hence latitude, has not previously been proposed as a limiting variable for *C. mopane* and is seldom considered important for subtropical species in general. Latitude co-varies with numerous additional variables (e.g. temperature, seasonality

etc.) other than day length and should therefore be interpreted with caution. We suggest, however that decreasing dry season day length can have a role in determining the distribution of this species. Reduced day length, alone, does not prevent the growth of *C. mopane,* as individuals are readily grown in nurseries and gardens south of this limit (*pers. obs.*). Instead, reduced day length in the dry season may act to limit the competitive ability of *C. mopane,* by reducing growing season length. Work on other savanna species shows that towards the end of the wet season, although photosynthesis takes place, above-ground growth ceases, which may reflect a shift in allocation to roots and reserves (Rossatto et al. 2009, Schutz et al. 2009). Shorter day lengths, south of *C. mopane*'s range, may act to reduce the time available for the storage of assimilates each winter (Wakeling et al. 2012) eventually reducing its ability to overcome demographic bottlenecks (Higgins et al. 2000), i.e. to rapidly escape the fire trap or to resprout and coppice after damage by herbivores, fire and frost (Holdo 2007, Schutz et al. 2009). We acknowledge that some caution should be exercised in interpreting the importance of these results, as these models are based on the distribution information obtained for the realized niche (for full review see Pearson and Dawson 2003) and allowing for the possibility that additional important drivers of this species' fundamental niche may not be accounted for.

Landscape distribution limits

At the landscape scale, detailed mapping revealed that edge and non-edge populations of *C. mopane* have a different distribution across hill slopes or catenas. This has not been described for this species before, and provides a clue as to what limits its distribution along its southern boundary at the landscape scale. The edge populations showed an exclusive preference for the mid-upper slopes, whereas the non-edge populations occurred along the entire slope. The absence of *C. mopane* from the crests, at both sites, is consistent with several previous studies which show that *C. mopane* is generally most abundant on clay-rich soils (Fraser et al. 1987, Timberlake 1995, Venter et al. 2003). Venter *et al.* (2003) suggest that the absence of *C. mopane* from crests is due to the shallow gravel and sandy soils that occur at that position in the soil catena. This, however, does not explain why *C. mopane* was completely absent from the clay-rich, bottomland soils in the edge populations. Rainfall is also unlikely to be responsible as the rainfall average of both sites is similar (Gertenbach 1983, LEDET 2008). Furthermore, the mean long-term rainfall of both sites falls within the preferred rainfall range for this species. While the fine-scale heterogeneity of soil moisture within these sites could vary widely within a small distance (Smit and Retman 2000), this is unlikely to be have been

significantly different between the two sites as the soil types, slope and underlying geology were almost identical between sites. We therefore suggest that the variance in soil moisture at a landscape scale is unlikely to be a factor that will explain the spatial distribution of *C. mopane* at the southern end of its distribution.

While soil type and water availability do not appear to explain the absence of *C. mopane* from the lower slopes at the edge site, it is plausible that minimum temperatures are limiting, consistent with the regional-scale model results. The average minimum temperature for the coldest month at the nearest weather station at the non-edge site is 9.1 ºC (Phalaborwa town) and 6.5 ºC near the edge site (Talamati camp, *South African Weather Service*). Although the temperature minimum at the edge site is higher than the 5 ºC threshold suggested by both Henning and White (1974) and our model, local relief can further reduce minimum temperatures via cold air drainage (katabatic) cooling at night (Venter et al. 2003). We propose that at the cooler edge site, stronger katabatic cooling in the drainage lines causes lower minimum temperatures, sufficient to exclude *C. mopane* from the lower slopes. The most likely mechanism for such a temperature constraint is the death of seedlings or saplings during the cold snaps in winter due to cold or frosting (Whitecross et al. 2012). The canopies of smaller plants are exposed to lower temperatures than those of adult trees, as the lowest minimum temperatures occur 15 cm above the ground (Bader et al. 2007). To our knowledge, there is little or no empirical investigation of minimum temperatures limiting the distribution of any tree species within a sub-tropical savanna, and investigations into *C. mopane* seedling growth and survival at temperatures below 20 ºC are absent from the literature (Choinski & Tuohy 1991) (but see Wakeling et al. 2012 for the effects of temperature on *Acacia* grow rates). This hypothesis is therefore worthy of further investigation for dominant species such as *C. mopane*, particularly considering the imminent increase in minimum temperatures resulting from climate change (New et al. 2006).

In addition to the location of *C. mopane* across a landscape, we also investigated the spatial patterning of *C. mopane* patches within this landscape. The structure of the patches differed between the edge and non-edge sites, with patches at the southern boundary being smaller, more numerous and more dispersed. This pattern is consistent with the spatial patterns of *C. mopane* in a semi-arid savanna in Botswana, where the distribution becomes patchy towards the distribution limits (Madams 1990) and with the general macro-ecological pattern of ranges becoming less continuous as they reach the periphery (Brown et al. 1996). Such a pronounced patchiness is often caused by strong abiotic constraints that are reinforced

by strong biotic feedbacks (Peters et al. 2006). As water availability may strongly limit the successful establishment events of *C. mopane* seedlings (Harrington et al 1991, Stevens *unpublished data*), establishment events are infrequent. Temperature at the southern edge, may act to differentially constrain establishment across the landscape, creating an initial patchiness in the population. This influence is further exacerbated as local heterogeneity creates and constrains extensive patchiness. For example; woody plants are more susceptible to the effect of below-average cold spells in open stands than in dense stands where they protect each other from the cold (Smit 1990). The abrupt patch edges also suggest positive feedback between individual trees and their biotic environment (Parmesan et al. 2005, Bader et al. 2007). Seedling establishment of *C. mopane* has been observed to be most successful in areas with low grass cover (Mlambo & Nyathi 2001) and the observed patchiness of adult trees may reflect previous patchiness of grass production and /or grazing. Provided they survive the winter temperatures, these seedling patches may become self-sustaining, as there is strong evidence that *C. mopane* saplings and adults facilitate the establishment of more seedlings by suppressing herbaceous vegetation (Smit 2001, van der Waal et al. 2009).

Conclusion

Our MAXENT model supports Rutherford et al (1999) prediction of a westward *C. mopane* expansion where minimum temperature is the critically limiting environmental variable along this edge. With a predicted increase in mean minimum night-time temperatures (0.6 °C – 1.16 °C increase) (Davis 2010), this boundary is likely to shift. However the predicted range shift southwards is not as strongly supported because day length was not considered by Rutherford et al, (1999), and our results suggest it is a potentially important interacting variable that can limit the extensive spread of *C. mopane* southwards. Our mapping at the landscape scale indicates that a smaller southward range shifts may still occur as minimum temperature maybe an important constraint in forcing a patchier population distribution.

In conclusion, this study provides the first detailed model of the environmental factors that may limit the regional distribution of *C. mopane.* Additionally this investigation into regional and landscape-level distribution patterns allows us to formulate testable hypotheses regarding the determinants of the range of a keystone species.

Acknowledgements

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Chapter 4: Increasing temperatures can improve seedling establishment in arid adapted savanna trees.

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NS conceived and designed experiments and models, conducted the experiments, analysed the data and wrote the manuscript. CES provided logistical support, access to facilties and financial contributions through accomdation and commented on the manuscript. WB, SA are supervsiors and provided supervisory support, both provided funding towards this project

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Abstract

Plant species are shifting their ranges in response to global change, thus intensifying the need to predict such changes accurately. As the environmental requirements controlling plant distribution act differently at all stages of development, a demographic-specific understanding on what determines these distributions should be adopted. Here we investigated the germination niche of two common savanna species *Acacia nigrescens* and *Colophospermum mopane*, to disentangle the direct and indirect effects of temperature on seed germination and establishment, and to explore the impact of higher temperatures on establishment success of savanna trees. Under laboratory conditions, we used thermal gradient plates (TGP) to determine the thermal germination niche of both species and a water stress experiment was conducted on *C. mopane* to account for water-temperature interactions. Using these data we parameterized a soil-moisture model to determine germination and establishment success under field conditions at current and future temperatures (+4 °C). Higher future temperatures did not limit germination directly, but reduced the number of germination events by reducing the time window of suitable available soil water. Conversely, warmer conditions will accelerate the rate of radicle extension and increase the frequency of seedling establishment events. An additional advantage is that fewer seeds will germinate, resulting in slower seed bank depletion when successful seedling establishment events do occur.

Keywords

Global change; demographic; temperature stress; drought stress, *Colophospermum mopane*

Introduction

Understanding the determinants and limits of species distributions is fundamental to ecology (McInnes et al. 2009; Parmesan 2006) yet, surprisingly, these determinants are understood for only a few species (Gaston 2009). Range shifts can have serious implications both for the conservation of focus species, and for the communities into which plants are moving. With increasing reports of plant, insect, and animal species shifting their ranges in response to changes in climatic conditions (Foden et al. 2007; Parmesan and Yohe 2003; Root et al. 2003), predictive understanding of these processes is critical. The limitations of correlative studies of climate and plant occurrence are well recognised (McMahon et al. 2011; Heikkinen et al. 2006)**,** yet our ability to replace them with more mechanistic approaches is constrained

by an inadequate insight into what determines where a plant will grow (Purves 2009). Factors controlling plant distribution act at all stages of development and the environmental requirements of seeds vs. seedlings vs. adult trees can be very different (Edkins et al. 2008; Midgley and Bond 2001). For example, *Tilia cordata*, in Britain, can survive and grow, but not produce viable seeds, in temperatures well below those that define its northern distribution limit. As the rate of pollen tube extension is strongly constrained by cool temperatures, seed production limits its northern expansion. In warm years however, fertilisation is successful, and all subsequent life history stages successfully survive cool temperatures (Pigot and Huntley 1981).

Seed germination, an early life history stage, is the first step in the successful establishment of a plant and hence will influence the distribution of a species (Donohue et al. 2010). Water and temperature are critical drivers of seed germination across all biomes (Walck et al. 2011): seeds need sufficient water to initiate root extension, and sufficient warmth and moisture for enzyme activation (Lambers et al. 1998). Moreover, temperature is an important cue indicating suitable environmental conditions for germination (Fenner and Thompson 2005). Additional biome specific factors also drive germination success. For example in tropical forests there is a light threshold, and in fynbos environments smoke is a common germination cue (Brown and Van Staden 1997). Where all the necessary germination cues are understood then accurate predictions can be made on the impact of climate change on this demographic stage.

In savannas, little is known about the germination niche of trees (Chidumayo 2008; Higgins et al. 2000; Baskin and Baskin 1998) and this limits our ability to predict future climate change impacts on savanna plant distributions. Numerous local characteristics such as high grass biomass and shade have been proposed to limit seed germination (Harrington 1991; Smith and Shackleton 1988; Walker et al. 1981). In the highly stochastic rainfall environments of savannas (Reason 2005; Kigel 1995), water availability is a major factor limiting early seedling success (Botha 2006; Higgins et al. 2000; Wilson and Witkowski 1998; Harrington 1991) and therefore the probability of seedling establishment (Botha 2006; Higgins et al. 2000). Tree seedling survival is critically dependent on the water availability in the upper layers of the soil and the capacity of the seedling to extend its radicle out of the upper, drier soil layer into the moister layers below the grass root and evaporation zone (February and Higgins 2010; Scholes and Walker 1992; Koop & Walker 1985). Rapid germination and radicle extension are crucial drought survival mechanisms to ensure

establishment before the surface layers of the soil dry out (Choinski & Tuohy 1991; Johnson et al. 1996).

Temperature is seldom explicitly discussed as an important component of germination in savannas or a factor influencing subsequent seedling establishment. Temperature can affect seedling establishment in two ways: firstly by directly controlling rates of germination and radicle extension, and secondly by indirectly controlling the rate of evaporation and the amount of time water is available in the upper soil layer. As predicted temperature increases in the interior of South Africa for 2100 are in the order of 4-6 ^{o}C (Engelbrecht et al. 2011), temperature effects on savanna plant establishment warrant more attention. It has been assumed that minimum temperatures are not low enough to prevent germination or lower survival during the growing season in (sub-) tropical savannas (Woodward 1987). Yet, this assumption has never been tested. Increased temperatures may enhance enzyme activity, thus accelerating both growth and radicle extension (Lambers et al. 1998). However, above an optimum temperature (T_o), increased environmental temperature will be detrimental, with the upper temperature limit (T_c) to germination defining seed death (Covell et al. 1986) due to irreversible changes such as protein denaturation (Wahid et al. 2007). With regards to the indirect effect of temperature on evapotranspiration, high rates of moisture loss could reduce the window of water availability in the upper layers of the soil thereby constraining the time available for radicle extension. Thus, higher temperatures could concurrently increase germination and growth rates, and reduce the time available for seedling establishment.

In this study, we determined the role of temperature in limiting germination and establishment of two common savanna tree species, *Colophospermum mopane* and *Acacia nigrescens*. Both species occur in savannas but have different distribution ranges (Palgrave 2002), which suggests different climatic preferences. *C. mopane* tends to occur in hotter and drier environments, and correlative studies suggest that some of its distribution is limited by cold temperatures (Rutherford et al. 1999; Burke 2006, Stevens et al. 2013), although the mechanisms and life history stage by which this species experiences limitation, climatic or otherwise, is not known.

Using thermal gradient plates (TGP) (Cochrane et al. 2011) we determined the thermal germination niche of both species and included a water stress experiment on *C. mopane* to account for water-temperature interactions. These data were then used to parameterise a model to determine germination and establishment success under field conditions given

current and future temperatures. This method allowed us to disentangle the direct and indirect effects of temperature and to produce meaningful predictions on the impact of higher temperatures on the future establishment success of these savanna trees.

Methods and Materials

Seeds were collected from two savanna species, *Acacia nigrescens* (Fabaceae) and *Colophospermum mopane* (Fabaceae). Seeds were gathered from random trees across their distributional range 6-9 months before the experiment took place. Seeds were air dried and then stored at 18 °C in brown paper bags until arrival at the Millennium Seed Bank, Wakehurst, UK, where seeds were transferred to 15 °C at 15% relative humidity until the experiment began.

Thermal requirement for germination

A bidirectional thermal gradient plate (TGP; Grant Instruments, Cambridge, UK) was used to measure the effect of temperatures on seed germination. The TGP was used to provide 30 alternating day/night temperature regimes and six constant temperatures ranging from 8°C to 36°C (Figure 1). As the constant temperatures on the TGP did not exceed 36 °C, seeds were also placed in a separate 40°C incubator to measure germination at this higher temperature. In all cases, seeds were exposed to a 12h photoperiod (white light with photon flux density of 50 W/m^2).

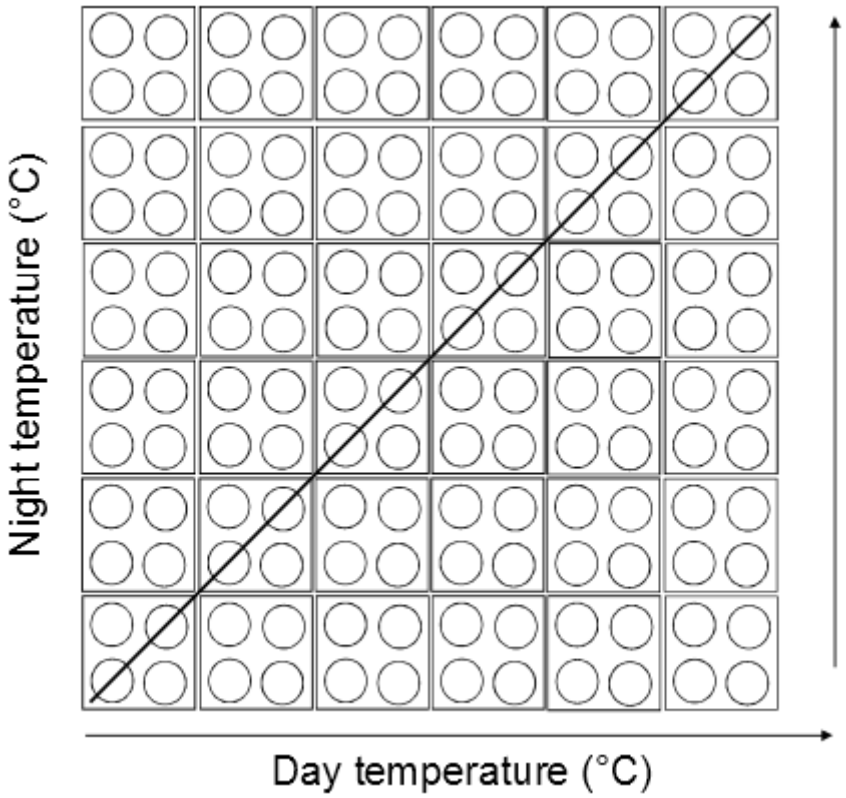

Figure 1: A bidirectional thermal gradient plate (TGP; Grant Instruments, Cambridge, UK) was used to measure the effect of temperatures on seed germination. Four Petri dishes (round circles) were placed in each temperature grid (squares) creating a grid of 36 temperatures. Temperatures alternated every 12 hours where the direction of the thermal gradient was reversed on each axis. Solid diagonal line indicates constant day/night temperatures.

A. nigrescens seeds were chipped to break any physical dormancy and sown on the surface of 1% w/v water-agar in 50 mm diameter Petri dishes. Four Petri dishes were placed in each temperature cell creating a grid of 36 temperatures (with 6 constant temperatures; Figure 1). At each temperature cell, 15 seeds of *A. nigrescens* and 12 seeds of *C. mopane* were placed. Due to the large size of the *C. mopane* seeds the germination run was replicated a second time, resulting in an overall total of 24 seeds per temperature cell. To determine the temperatures experienced by the seeds, five thermometers (Grant Instruments, Cambridge, UK) were embedded in 1% agar-water in petri-dishes and placed at each corner and the centre of the TGP, recording every 10 minutes for the duration of the experiment. Germination was scored twice daily for the first three days and thereafter scored daily until no germination had taken place for two consecutive days. Germination was considered successful when 1 mm of the radicle protruded from the seed coat. Seeds were moved to Petri dishes containing fresh agar as necessary to prevent drying.

Water potential requirement for germination

C. mopane has a wide environmental range and is often the dominant tree in arid savannas (Timberlake 1995). Consequently we studied the interaction of temperature and drought stress on seedling germination and subsequent radicle extension in *C. mopane. S*eeds were exposed to 20 and 30 °C across five water potentials 0 (control), -0.1, -0.4, -0.7 and-1 MPa created by using polyethylene glycol 6000 (PEG; Fisher Scientific UK, Loughborough, UK). The desired water potential was determined using the temperature dependent equations described by Michel (1983) to calculate the amount of PEG to be added to water. Seeds were placed on germination paper in transparent re-sealable plastic boxes (17 x 12 x 5cm) which was moistened with 14ml PEG solution. To prevent alteration of water potential, the ratio of PEG solution volume: filter paper weight was kept greater than 12 (Hardegree and Emmerich 1990). PEG solutions were replaced in each germination box every 48 h. Germination was scored on a daily basis and was considered successful when 1 mm of the radicle protruded from the seed coat. On the day of germination the radicle length was recorded. Radicle length was then recorded every second day thereafter for 10 days.

Data Analysis

Thermal time modelling

The effect of temperature on germination can often be described by the thermal time model (Bierhuizen and Wagenvoort 1974). Threshold temperatures T_o and T_c were calculated from the germination rate data for 50 % of the final proportion of seeds to germinate following the methodology of Covell et al. (1986) and Hardegree (2006) (see Appendix A1 *for full model* details). For each species, the thermal time (θ_T) to germination G, at sub-optimal temperatures was calculated as:

$$\theta_{T(G)} = (T_G - T_{bG})\, t_G \qquad \text{equation 1.}$$

where T_G is the actual temperature, T_{bG} is base temperature as determined from a repeated probit analysis and t_G time since start of imbibition (Covell et al. 1986). The repeated probit analysis (Bradford 1990) was performed in Genstat (version 11.1.0.1575, VSN International Ltd, UK) on germination values and their corresponding log-thermal time [$\log_{10} (T_g - T_{bg})\, t_g$], varying the value of T_{bG} until the best fit was obtained, using the following equation (Daws et al. 2004; Bradford 1995; Covell et al. 1986)

$$\text{probit}\,(_G) = \{\log [(T_G - T_{bG})\, t_G\,] - \log [\theta_T(50)]\}/\sigma_{\theta T} \qquad \text{equation 2.}$$

Where probit ($_G$) is the probit transformation of the cumulative germination ($_G$), $\theta_T(50)$ is the median thermal time to germination and $\sigma_{\theta T}$ is the standard deviation of log θ_T (50). Data points where germination did not increase for more than three consecutive days were excluded from the analysis.

Hydrotime modelling

Seed germination responses to water potential can be described on a hydrotime scale (Gummerson 1986). The hydrotime for each water stress treatment was calculated using the methodology described by Gummerson (1986) and Bradford (1995). The hydrotime (θ_H) for fraction *G* of the population to germinate at each water potential temperature was calculated as:

$$\theta_{H(G)} = (\Psi_G - \Psi_{bG})\, t_G \qquad \text{equation 3.}$$

where Ψ_G is the water potential, Ψ_{bG} is base water potential as determined from a repeated probit analysis and t_G time since start of imbibition (Bradford 1995; Gummerson 1986). The repeated probit analysis was applied where all Ψ_G were regressed against $\Psi_G - (\theta_H / t_G)$, until the best fit was obtained (Bradford 1990), according to the equation (Eq 4):

$$\text{Probit (g)} = [\Psi_G - (\theta_H / t_G) - \Psi_b (50)]/\sigma_{\Psi b} \qquad \text{equation 4.}$$

where $\Psi_b(50)$ is the median of Ψ_b, and $\sigma_{\Psi b}$ is the standard deviation in Ψ amongst the seeds within the population.

Radicle extension

Unequal germination between treatments resulted in radicle length data with an unbalanced design. Data were analysed using linear-mixed effects models in the nlme package (Pinheiro et al. 2007) for R (R Development Core Team 2012). Model selection was performed by constructing a full model in which all fixed predictors and their interactions were present and subsequently removing all non-significant terms. The germination box was initially included as a random variable, but as its contribution to the models was extremely small the analysis was performed without random variables using the generalised least squares model. Significance of fixed terms was determined with marginal l F-tests (Pinheiro and Bates 2000).

Modelling seedling establishment under field conditions

The experimental results were linked to climatic data from a seed-collection site in the south of the range of *C. mopane* (Phalaborwa in Limpopo Province, South Africa). The Phalaborwa climate is characterised by hot , wet summers and mild and dry winters, with a mean summer temperature of 24 °C, a mean winter temperature of 18.5 °C and a mean annual rainfall of 481 mm (Schulze 2007; South African Weather Service, Phalaborwa station). The aim was to determine the frequency of successful establishment events by using the thermal time and hydrotime parameters to estimate the germination rate and rate of radicle extension under temperature and soil moisture conditions experienced in the field. A full range of micrometeorological data have been measured at the Malopeni flux site near Phalaborwa for three years (from 2009-2011). These data were used to simulate current conditions and the temperature record was increased uniformly by 4 °C to simulate an extreme future temperature regime for 2100 (Engelbrecht et al. 2011). As predictions of future rainfall patterns in this region are very uncertain (Engelbrecht et al. 2009), rainfall was kept constant.

In the model, germination and seedling establishment are driven by temperature and soil moisture (measured in MPa; see Appendix A.2 *for full description of germination and establishment modelling*). The soil moisture input was determined using a simple two-layer water-balance model (Appendix A.3 *for full description of soil moisture model*) where water held in the upper (90 mm) layer was accessible to direct evaporation from the soil surface as well as transpiration, and water in the lower layer could only be lost by transpiration. Seedlings were considered to have established when their radicles extend to the lower layer (> 90 mm long).

Once the first significant (>15ml) rainfall event of the rainy season occurred, a potential germination event was initiated. Germination was considered completed once a seed had accumulated sufficient heat, as defined by it reaching $\theta_{T(50)}$ (equation 1) and moisture, by reaching the required $\theta_{H(50)}$ (equation 3). We assumed that if seeds did not germinate due to insufficient $\theta_{T(50)}$ or $\theta_{H(50)}$ they were still available for future germination events.

After germination, radicles grew at a rate determined from the measured radicle extension rate, determined by the modelled soil moisture and temperature for each day. At wilting point plants are no longer able to take up moisture from the soil and the same was assumed for the seeds. Wilting point can vary from plant to plant but is traditionally set at -1.5 MPa. Although savanna plants almost certainly have a lower wilting point, using a lower value makes little

difference to the θ_{WP} since the θ - ψ relationship is very steep in this region of the curve (Lambers *et al,* 1998). Once the soil reached wilting point (< -1.5 Mpa), root growth was stopped, and the counter was reset back to t_0. If the radicle was less than 90mm it was considered a failed establishment event. If the radicle was longer than 90mm we considered the establishment event successful. This model was run for three years (2009, 2010 and 2011).

Results

Thermal requirement for germination

A. nigrescens and *C. mopane* had highest germination success when daily temperature averages were greater than 20 °C, with a maximum total germination of 93 % (at 30.2 °C) and 100% (at 23.1 °C) respectively (Figure 2). Below 20 °C germinability was less than 50 % in both species. Near equal germination percentages occurred on either side of the constant temperature line, indicating that it was insignificant whether a seed experienced a particular temperature during the day or night. Above 20°C, 50 % of the seeds germinated within 5 days for both species.

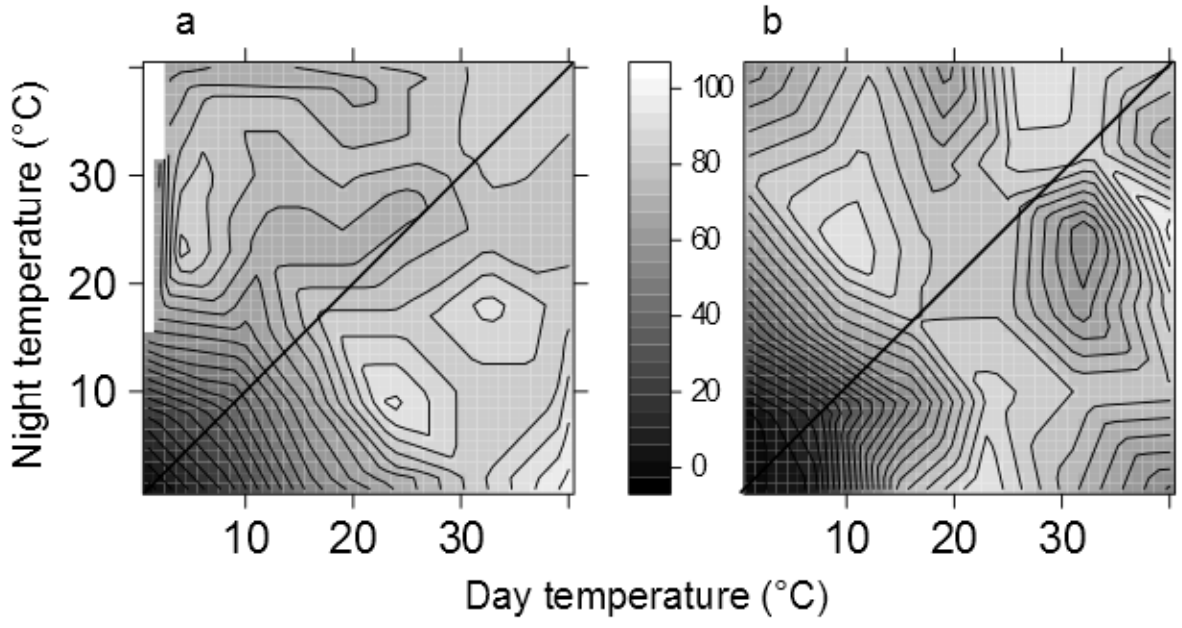

Figure 2: Contour plots, with points of equal percentage germination connected by germination isopleths, for seeds of a) *C. mopane* and b) *A. nigrescens* . The shaded block in between the graphs gives the colour code for germination percentage, ranging from dark (low germination) to light (high

germination). Germination percentage was calculated from the germination success in each temperature cell in the TGP.

Temperature thresholds were calculated from the germination data. *A. nigrescens* had a T_b of 13.3°C, T_o of 33.9 °C and T_c of 43.6 °C (Table 1). *C. mopane* had an equally wide temperature range, ranging from T_b of 11.6 °C to a T_c of 43.6 °C, with a T_o of 34.1 °C (Table 1). The thermal time model predicted that *C. mopane* had a $\theta_{T(50)}$ of 25.6 °Cd ($R^2 = 0.58$) and for *A. nigrescens*, $\theta_{T(50)}$ was lower at 16.9°Cd ($R^2 = 0.60$). The model over-estimated the final cumulative germination values for *C. mopane* but captured the final germination values for *A. nigrescens* except at 30 °C (Figure 3). The thermal time models for both *C. mopane* and *A. nigrescens* captured the slope of the response (Figure 3), which was critical for the germination and seedling establishment model (see below).

Table 1. Parameter estimates of the thermal time model (sub-optimal temperatures) for *Acacia nigrescens* and *Colophospermum mopane*. The germination parameters T_o (optimum temperature) and T_c (ceiling or maximum temperature) were calculated by plotting the reciprocal of the time for 50 % of the final proportion of seeds to germinate against temperature (see Appendix 1 for details). The parameters; T_b (base temperature), $\theta_{T(50)}$ (thermal time for 50% of the seeds to germinate), K (intercept of the constant) and σ (the standard deviation of $\theta_{T(50)}$) were determined using a repeated probit analysis of germination against their corresponding log-thermal time values. n (number of data points), P and R^2 are of the probit model.

	Threshold temperatures			Thermal time parameters					
Species	T_b (°C)	T_o (°C)	T_c (°C)	K	$\sigma_{\theta T}$	n	P	R^2	$\theta_{T(50)}$ (°C.d)
A.nigrescens	13.3	33.9	43.6	-4.53	0.27	98	P<0.001	0.60	16.9
C.mopane	11.6	34.1	43.6	-2.78	0.51	244	P<0.001	0.58	25.6

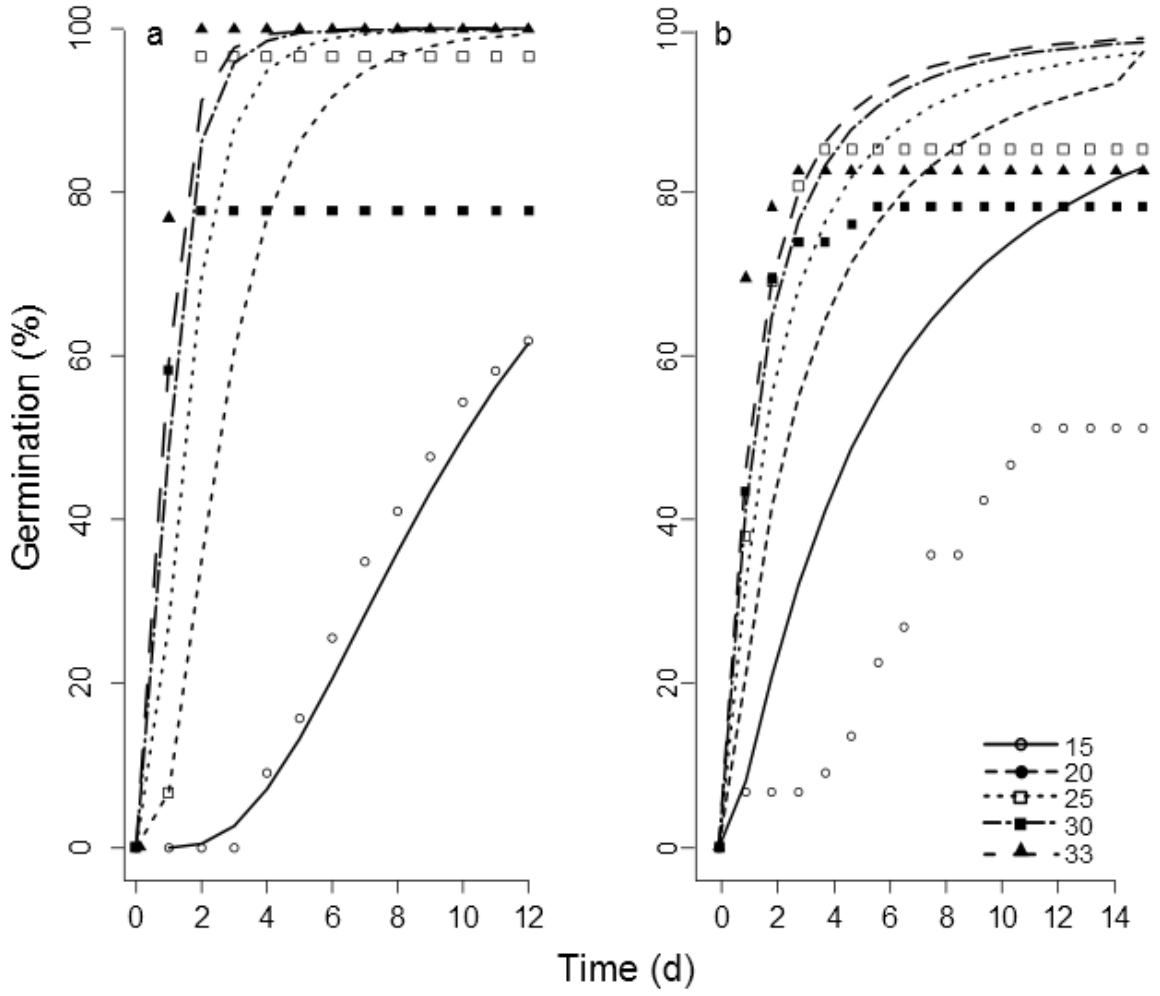

Figure 3: Thermal time models for a) *A. nigrescens* and b) *C. mopane*. Germination data are included for only points falling within 1°C of the specified temperatures. Solid lines indicate model fit and points indicate cumulative germination for each temperature. Predicted outputs were calculated from the following equation with constants derived from the repeated probit analysis probit $(_G) = \{\log [(T_G - T_{bG})\ t_G\ ] - \log [\theta_T(50)]\}/\sigma_{\theta T}$.

Water requirement for germination of C.mopane

Overall, seeds exposed to the lowest water potentials had reduced germination rates and the lowest total amount of successfully germinated seeds (Figure 4). The hydrotime models for

both temperatures gave a good fit (R^2 = 0.78 for 20 °C and R^2 = 0.73 for 30 °C) accounting for a large amount of the variation. Only at -0.4 MPa, at both 20 °C and 30 °C, did the model over-estimate and underestimate the germination response, respectively (Figure 4). Seeds exposed to the 20 °C treatment had a higher $\theta_{H(50)}$ than the 30 °C treatment (1.4 MPa d and 1.0 MPa d) and thus required more exposure time to moisture to germinate (Table 2). Higher temperatures improved the tolerance of seeds to higher water stress as demonstrated by the $\Psi_{b\,(50)}$; 50 % of the seeds within a population could germinate in a water potential as low as -0.79 MPa when exposed to a daily average temperature of 30 °C, but when seeds were exposed to a lower daily average temperature of 20 °C, 50 % of the population did not germinate below a water potential of -0.51 MPa (Table 2).

Table 2. Parameter estimates of hydrotime model for *Colophospermum mopane* as determined from a repeated probit analysis. $\Psi_b(50)$ is the median of Ψ_b, and $\sigma_{\Psi b}$ is the standard deviation in Ψ amongst the seeds within the population. K is the intercept of the constant and σ is the standard deviation of the response. n (number of data points), P and R^2 are of the probit model.

Treatment	$\Psi_{b(50)}$ MPa	$\theta_{H\ (MPa\ d)}$	$\sigma_{\Psi b}$	K	n	P	R^2
20 °C	-0.41	1.4	0.50	0.83	139	P<0.001	0.78
30 °C	-0.79	1.0	0.61	1.28	53	P<0.001	0.73

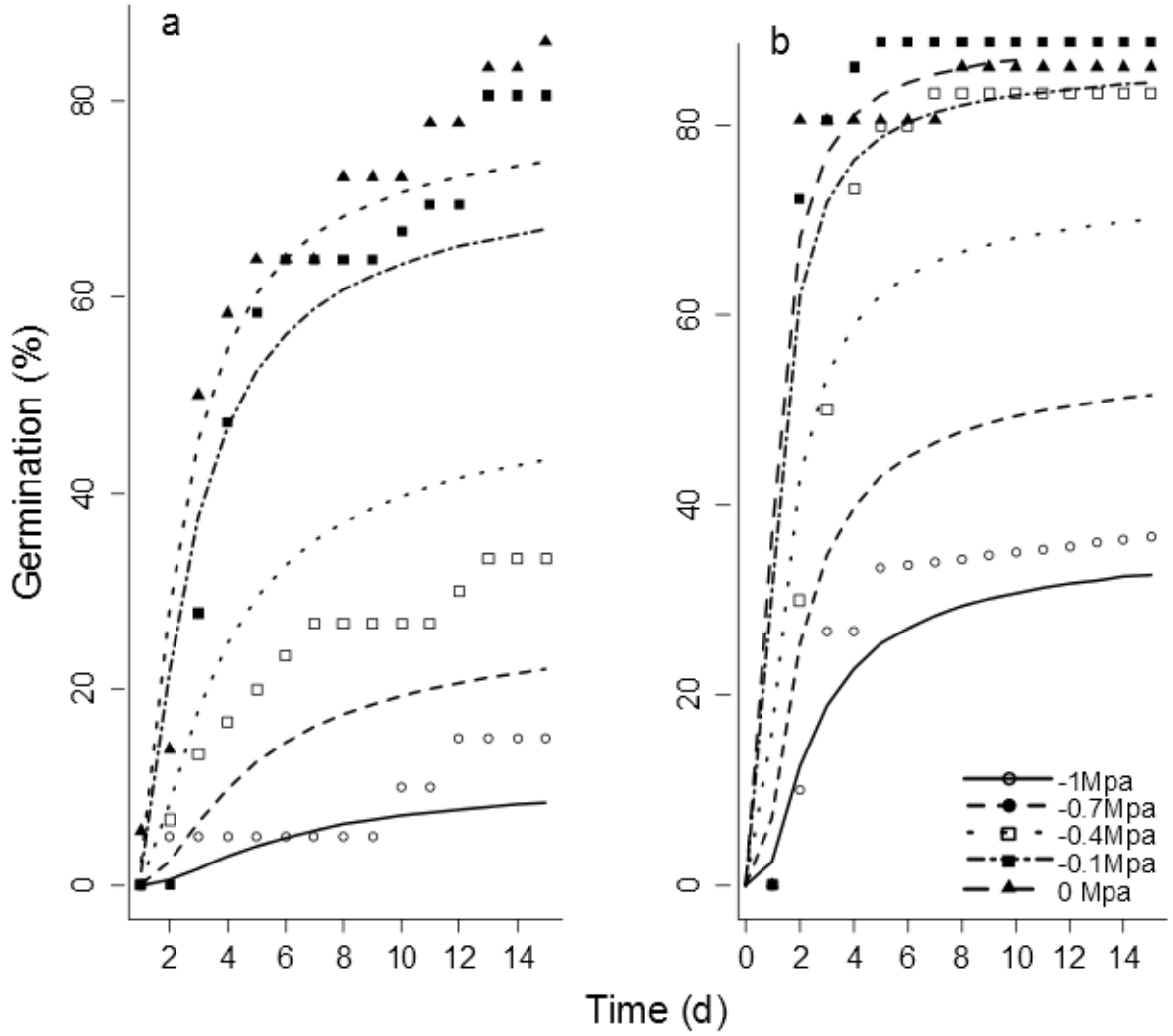

Figure 4: Hydrotime models for *C. mopane* at two temperature treatments, (a) 20°C and (b) 30°C. Points represent the individual treatments and associated lines represent the hydrotime model fit. The predicted lines were calculated using the constants derived from the repeated probit analysis probit (g) = $[\Psi_G - (\theta_H / t_G) - \Psi_b(50)]/\sigma_{\Psi b}$. $n_{30°C} = 52$; $n_{20°C} = 139$.

After 10 d of radicle growth, the final radicle length was best explained by a regression model that included water potential ($F_{1,184} = 26.81$, $P < 0.001$) and temperature ($F_{1,184} = 7.05$, $P < 0.001$). At any water potential, radicles grown at 30°C grew faster (mean radicle extension = 4.7 mm/day) and were longer than those grown at 20°C (mean radicle extension = 2.5 mm/day) (Figure 5). Moreover, while increasing water stress always reduced radicle growth rate at 20 °C, at 30 °C water potentials as low at -0.4 MPa resulted in similar radicle lengths as the non-water stressed treatment (Figure 5).

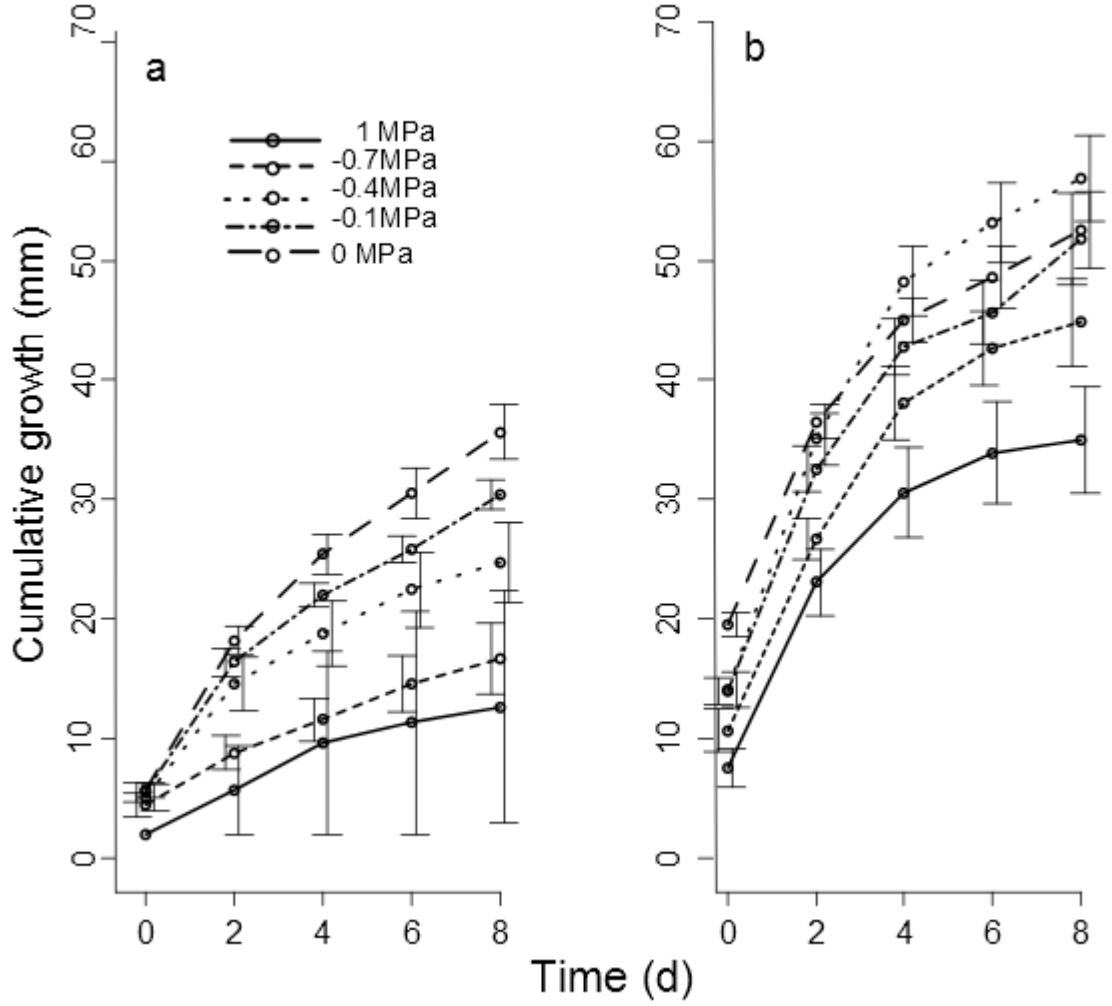

Figure 5: Daily radicle growth over 10 days following germination at a) 20 °C and b) 30°C , in five different water stress treatments (0, -0.1, -0.4, -0.7, -1.0 MPa) for *C. mopane*. Values are means ± standard error ($n_{30°C}$ = 112, $n_{20°C}$ =87).

Germination and seedling establishment model

The soil moisture model, using current temperature scenarios, indicates that germination events were not limiting (Figure 6). Across all years for current temperatures, multiple germination events were predicted during the wet season (total = 42). Although germination events were rare in the dry season, they did occasionally occur. Under elevated temperature conditions of +4 °C, fewer germination events were predicted (total = 31). While germination events were common, successful establishment events where the seedling radicles could grow > 90 mm before water loss were few. Over the three year period under

current climatic conditions, only two successful seedling establishment events were simulated. Under warmer conditions however there were five successful establishment events simulated over three years. Successful establishment events usually occurred when there were 24-28 days of soil moisture greater than -1.5 MPa, any value more negative than -1.5Mpa was too dry for seedling survival.

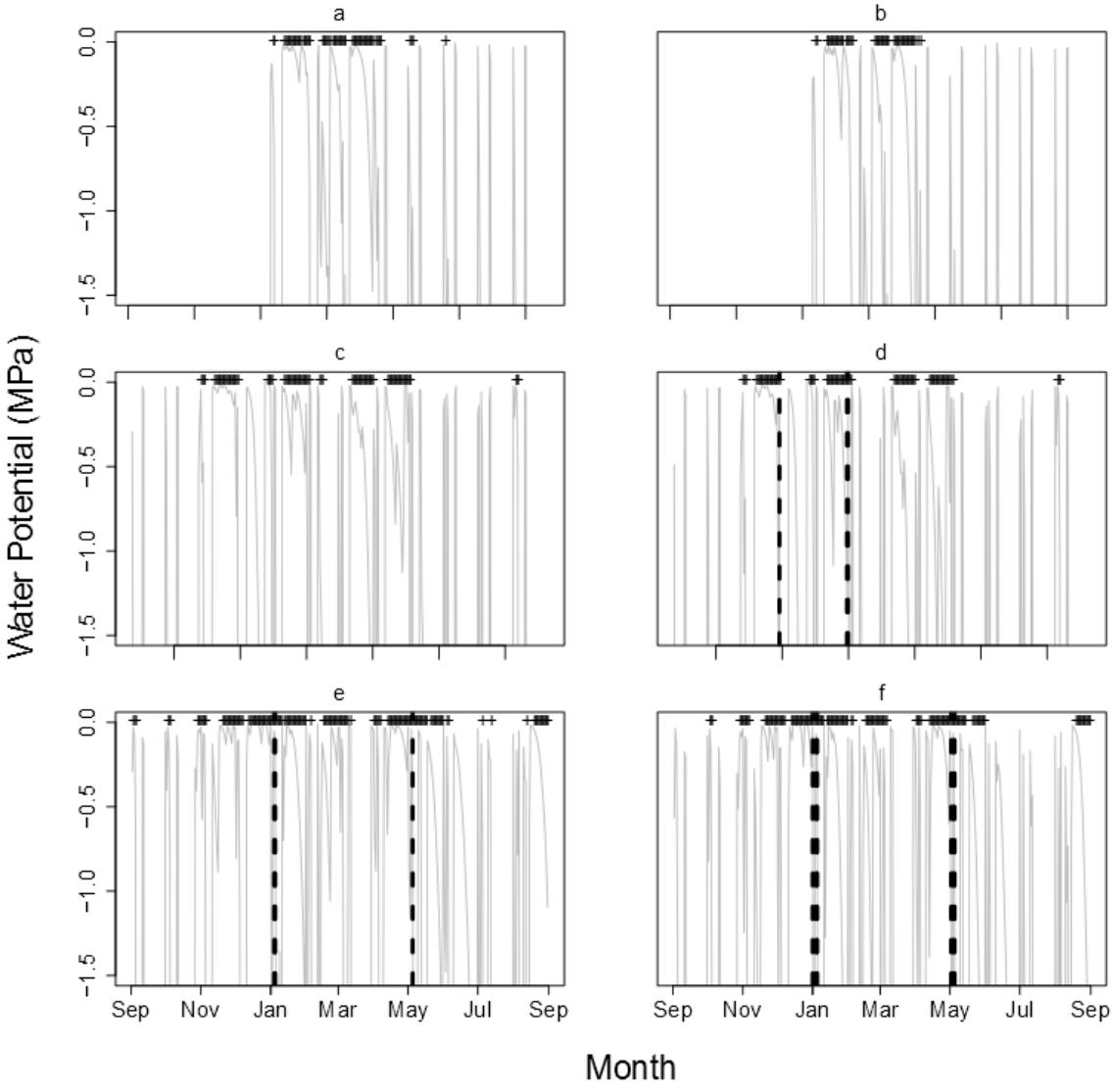

Figure 6: Modelled germination events and seedling establishment events for *C. mopane* across 3 years. Graphs on the left show outputs from measured temperatures for 3 separate years. Graphs on the right show regeneration events assuming temperatures for a particular year were 4°C warmer. From left to right; a) 2009 b) 2009 conditions +4°C, c) 2010, d) 2010 conditions +4°C, e) 2011, f) 2011 conditions +4°C . Successful germination events occurred when $\theta_{T(50)}$ (25.61°C d) and $\Psi_{b(50)}$ (1.4 MPa) were accumulated by the seeds. Successful seedling establishment occurred when temperature and soil moisture environment was sufficient to ensure radicle extension to 90mm before

the soils dried out. Pale grey lines indicate daily soil moisture (MPa), black plus signs at top of the graph indicate successful germination events and thick black dashed lines indicate successful seedling establishment events. Refer to A.3 for detailed methodology.

Discussion

Direct effects of temperature on savanna seed establishment

We demonstrate that the direct effects of temperature on the germination of the savanna species *C. mopane* and *A. nigrescens* are unlikely to limit their germination. The thermal optimum of germination (~34°C) and temperature range for high germination success (20-34°C) are within the range of typical environmental conditions during the growing season (Schulze, 2007) (mean annual temperature range 20.5 – 27°C). In spite of different geographic distributions, the germination temperatures for both species were similar; both displaying a wide temperature range (11-40 °C). The few existing studies from African savannas and the tropical savanna of Brazil, the Cerrado, confirm that seed germination of savanna species seldom occurs below 10°C, and is optimal at temperatures between 20°C and 35°C (Choinsky and Tuoy 1991 (for *C. mopane*); Baskin and Baskin 1998; Hoffman 1996; Felippe and Silva 1984)

Thermal time is an ecologically useful value that indicates the amount of heat sum units (°C) a seed must accumulate for 50% of the seed population to germinate (Covell et al. 1986). The thermal time models demonstrated that *C. mopane* and *A. nigrescens* germinate rapidly when water is unrestricted; given typical daily average temperatures in the growing season 50% of seed germination will occur within two days. Rapid germination (i.e. within 1 – 3 days) is a common occurrence for arid adapted plants (Kos 2010; Jurado and Westoby 1992; Elberse and Brennan 1990), allowing seeds to take advantage of a short and infrequent window when water is available. Choinsky and Touhy (1991) found that at 30°C, 90-100% of seeds germinated within 4-5 days for the savanna species *C. mopane, Acacia tortilis, Acacia karoo* and *Combretum apiculatum*. In moister, cooler grassland environments in southern Africa, these germination rates can be up to five times slower (Weiersbye and Witkowski 2002).

An important additional strategy employed by *C. mopane,* when grown at 30°C, was the higher tolerance to water stress (as demonstrated by lower ψb), and higher germination at every water potential tested (Figure 4), when compared to the same responses at 20° C. At

higher temperatures and under moderate water stress (-0.4MPa), radicle extension rates and length were increased, indicating an interactive effect between these two drivers. The model of this response does not follow Bradford's hydrothermal time model which assumes that ψb is constant at sub-optimal temperatures (Bradford 2002), which explains why the hydrotime model over and under-estimated the response at -0.4MPa at 20 and 30 °C respectively. Thus the thermal time and hydrotime were considered as independent parameters in the field model. The promotion of root growth under moderate water stress of between -0.14 MPa to -0.51 MPa was also found in other studies on *C. mopane* at 30° C (Choinsky and Tuohy 1991; Johnson and Pritchard 1996). It might be expected that this behaviour is common amongst drought tolerant species; however, it is not widely recorded in other savanna species (Choinsky and Tuohy 1991), nor many other arid species (Everitt 1983; Villabos, 2001). These root characteristics are considered to contribute to drought resistance (Nguten and Lamant 1989), although it is unknown what the resource allocation trade off is.

An arid germination strategy

The germination and seedling establishment response of the study species, to direct temperature and water stress, displayed three clear germination characteristics: 1) high germination percentages over a 20-35 °C temperature range; 2) rapid germination rate, and 3) for *C. mopane*, increased tolerance to moderate water stress at 30 °C. The combination of these three germination characteristics, an 'arid germination strategy', can be considered adaptive in hot arid environments where regular rainfall events are infrequent and continuously wet conditions are uncommon (Scholes and Walker 1992). The strategy enables rapid germination following a rainfall event, with rapid radicle extension in soils that dry quickly in these warm environments and thus impose a moderate water stress.

Indirect effects of temperature on savanna seedling establishment

Modelling germination and seedling establishment in the field

The thermal time and hydrotime were used to parameterise a model to determine germination and seedling establishment under field conditions in current and future temperatures. The model of field conditions (Figure 6) showed important indirect effects of temperature on germination and establishment success. Under current temperatures, germination events are not limiting and occur frequently throughout the growing season, but establishment events

are rare. With increased temperatures (+4°C), the number of germination events are predicted to be lower. This can be explained by increased evaporation, decreasing the amount of water available in the upper soil and thus decreasing the amount of time available for seeds to reach the hydrotime and thermal time thresholds before water is unavailable. However, when germination does occur, higher temperatures have a strong positive effect on the subsequent radicle extension rate, to the extent that the number of establishment events is predicted to increase under higher temperatures. This finding gives an adaptive explanation for the counter-intuitive interaction between high temperatures and water stress which was experimentally observed.

Germination and seed supply under modelled conditions

Understanding of the arid germination strategy and the high number of germination events that occur in the model raise the issue of seed supply in limiting the future spread of *C. mopane*. If the initial germination event is not followed by suitable environmental conditions, e.g. rainfall (Jurado and Westoby 1992), germination failure can result in a rapid depletion of the seed bank, thus creating a potential additional limitation to seedling establishment. Therefore there is likely to be a trade-off between high germinability and maintaining a seed bank to initiate several germination events through the season. Seeds of *C. mopane* do not have a long-term seed bank (Mlambo 2001), and seeds do not survive for more than a year in the field (Mojeremane and Kgati 2005; Mlambo and Nyathi 2002; Jordaan and Wessels, 1999), although they may have a degree of canopy seed storage (unpubl results from Wessels in Jordaan and Wessels 1999). The seeds are prone to environmental and fungal degradation (Jordaan 2001) and therefore are unlikely to persist on the tree for the entire wet season, though this strategy can counteract the loss of the entire seed bank to some degree. Therefore the arid germination strategy can only be maintained when the number of rainfall events occurring in an area is infrequent. As these rainfall events become increasingly frequent (e.g. in mesic savannas) then spreading the risk over several rainfall events and delaying germination may be advantageous. Although germination events are not limiting recruitment in arid savannas (< 450mm mean annual precipitation (MAP)), the model highlights that a limitation may occur at the seedling establishment stage (Higgins et al. 2000), with simulated establishment occurring in one out of three years under current climatic conditions. In savannas, it is often suggested that episodic or pulsed recruitment dominates and is only likely to occur during years where there is above average rainfall (Kraaij and Ward 2006; Wilson and Witkowski 1998; O' Connor 1995; Medina and Silva 1990; Chesterfield and

Parson 1985). Our model simulation outputs agree with this, and produce similar outputs to reported recruitment rates from South African savannas. Botha (2005), concluded that every 3.5 years were suitable for a large seedling establishment event (Kruger National Park, MAP = 546mm), whereas in the wetter Nylsvley (MAP = 623mm (Scholes and Walker 1992), one in two years are potentially suitable for establishment events (Wilson and Witkowski 1998).

Summary

Limitations to the current and future range of these arid adapted species include both direct and indirect effects of temperature. Higher temperature may improve the frequency of seedling establishment, thus raising the chance that given warmer temperatures, the range spread of *C. mopane* into previously unavailable cooler areas is possible. Higher rainfall can act to reduce and potentially limit seed supply through a higher frequency of unsuccessful germination events. This confirms previous studies which suggest that increasing mean annual rainfall can potentially limit the distribution of *C. mopane* (Stevens et al. 2013; Henning and White 1974), though a potential mechanism through which limitation occurs has not been previously suggested. This study highlights potential hurdles and opportunities that arid-adapted trees will meet when faced with climate change induced range shifts.

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Chapter 5: Transplant experiments fail to support climate factors as limits to savanna tree distribution

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NS &WB conceptualised the idea, NS designed the experiment and performed field work. SA commented on drafts, provided funding and advised on statistics. WB provided funding, and commented on drafts

Abstract

Dramatic changes are predicted for African savannas as a result of elevated CO_2 and climate change. Species are predicted to undergo large range shifts and expansions. Our confidence in these predictions is hindered by a poor understanding of what determines the distribution limits of common savanna species. Climate is widely assumed to be the primary factor that drives species distributions and climate variables are the key predictors in species distribution models. We present the first attempt to experimentally explore the climatic limits of African savanna tree distribution by determining tree growth and survival at a range of latitudes and altitudes much broader than the distribution limits of our study species. We planted *Acacia nigrescens* and *Colophospermum mopane* seedlings at four paired, high and low elevation sites across an 850 km latitudinal gradient. At each site seedlings were planted in both grassy and cleared plots. Rainfall, temperature and site location inside or outside their distribution range did not explain species distribution. Grass competition was the only variable that significantly affected plant growth rates, but grass competition alone could not explain the distribution limit. Species distributions were best predicted when maximum tree growth rates were considered in relation to local fire return intervals. The probability of sapling escape from the fire trap was the most likely determinant of distribution limits of these two species. As trees grew and survived 100s of kilometres south of their current range limits we conclude that climate does not directly limit the current distribution of these trees, and that climate change adaptation strategies for savanna environments based only on climatic envelope modelling will be inappropriate.

Introduction

The fundamental niche defines the environmental space where a species could occur in the absence of biotic interactions (Huchinson, 1957), and the realised niche defines where a species does occur. Understanding the determinants of these niches has been a major focus in ecology for many years (MacArthur, 1975; Woodward, 1987, Hubbell, 2001; Gaston, 2003). A renewed interest has been sparked by the threat of climate change induced range shifts (Parmesan & Yohe, 2003; Sexton et al, 2009), as climate sets the fundamental niche for many species (Woodward, 1987; Gaston, 2003; Rosenzweig et al, 2008; Thomas, 2010), and shifts in distributions are often consistent with those predicted from changing climates (Parmesan & Yohe 2003; Rosenzweig, et al. 2008; Thomas, 2010). Therefore both long-held assumptions and, more recently, observed species shifts have led to the development of predictive species

distribution models (Busby, 1991). These models aim to infer species distribution from correlations with climatic variables. However as they are intrinsically correlative they suffer the usual drawbacks of whether correlates with climate variables are also causal. Although a newer suite of studies of plant distribution and range shifts have become more mechanistic and have increasingly started examining the effects of demography (Kearney & Porter, 2009), biotic interactions (MacArthur, 1972; Wisz et al, 2013; Van der Putten et al, 2010) and dispersal limitation on species ranges (Svenning & Skov, 2007), the underlying assumption, that climate sets species distribution limits, is common. As these models are useful for large scale predictions they are used as a tool to explore climate change scenarios and are often used in shaping climate change policies, including in South Africa (DEA, 2011).

Although the distribution of the biomes of the world are generally correlated with climate (mean annual temperature and precipitation), some biomes are not. Whittaker (1975) identified a climate zone where vegetation structure was highly variable, and areas of grassland, savanna or tropical forest can co-occur (Whittaker, 1975; Bond & Keeley, 2005, Lehmann et al, 2011). Bond (2005) labelled Whittaker's climate zone as 'ecosystems uncertain' because vegetation structure and biomass is neither predictable by climate nor at equilibrium with it (Bond, 2004; 2005a). An alternative explanation is that the structure of these systems is under consumer control, i.e. fire and herbivory (Bond & Keeley, 2005; Bond, 2005), where fire and herbivory consume and modify the vegetation structure to keep it below its climatic potential. Therefore how does the traditional climate based framework explain plant species distribution in consumer controlled savanna systems where climate does not directly predict biome structure?

Temperature is often cited as the primary climatic variable that sets a species' fundamental niche and/or its current range boundary especially in temperate and high latitude ecosystems (Pigot & Huntley, 1981; Parmesan et al, 1999, Lenoir et al, 2008). Understanding the range boundaries of tropical species is acknowledged to be more complicated as biotic interactions and water availability are important additional drivers (Woodward 1987; Jolly, et al. 2005; Foden et al, 2007; Thomas 2010). Furthermore, within this context, African savannas occur across a rainfall gradient and depending on where they occur the limits of tree cover can be climatically limited (stable) or consumer controlled (unstable) (Sankaran et al, 2005). In "stable" (<650 mm) savannas water availability limits maximum woody plant cover (Sankaran et al, 2005) and the strongest plant demographic bottleneck to increasing adult

population size is likely to be at the seedling establishment phase where establishment opportunities are limited by drought (Harrington, 1991; Higgins et al., 2000). In unstable, mesic savannas (~>650mm MAP) top-down drivers are likely to limit mature tree population establishment (Williams et al, 1999; Higgins et al, 2000; Hoffman & Solbrig, 2003; Sankaran et al., 2005; Staver et al, 2011). Here, the critical population bottleneck is often at the sapling stage, although at the highest rainfall savanna end, grass productivity may be so high as to limit seedling establishment through grass competition. High grass productivity fuels frequent fires and traps saplings in the grass layer, where they are vulnerable to further topkill-inducing fires and herbivory (Higgins et al, 2000; Hoffman & Solbrig, 2003; Archibald et al, 2009; Lehmann et al, 2009; Prior et al, 2010; Midgley et al, 2010; Werner & Prior, 2013). These fires seldom cause mortality, but can prevent trees from progressing to larger size classes. (Frost, 1984). Importantly these suppressed saplings are not reproductive and repeated topkill can prevent the recruitment of reproductive individuals, which would eventually lead to local extinction (Higgins et al, 2000, Higgins et al, 2012). When trees exceed ~3m in height, they will often be sufficiently fire proof to be released from the fire trap (Bond, 2008; Wakeling et al, 2012).

While it is undeniable that climate shapes the ranges of many species, can consumer controls such as fire have a similar role in consumer-controlled savannas? Fire and mammal herbivory have clearly been shown to impact ecosystem structure but have not been explicitly considered as alternative large scale drivers of savanna tree species distribution. At the small scale, fire and herbivory have been noted to alter species composition so that, for example, herbivores can cause local species extinction or alter the density of plants in an area (Cumming, 1982; Prins & van der Jeugd, 1993; Augustine & McNaughton, 1998; Bond & Loffell, 2001; Werner et al, 2006; Woodward 1987; Jolly, et al. 2005; Foden et al. 2007; Thomas 2010). Fire regimes can also alter the community composition (Trapnell, 1959; Hoffman et al, 2004, Bond et al, 2005). For example, fire exclusion, besides increasing tree height and cover, can increase the number of fire sensitive species e.g. evergreen species in a community (Trapnell, 1959; Jose & Farinas, 1983; Carson & Abbiw, 1990; Shackleton & Scholes, 2000; Higgins et al, 2007; Plas et al, 2013).

As many studies demonstrate that species range limits occur across a climatic gradient we tested if climatic factors explained the distribution of two dominant savanna trees; *Acacia nigrescens* and *Colophospermum mopane. A. nigrescens* occurs in semi-arid savannas and is

widely distributed across South Africa. *C. mopane* is an arid savanna species which has a distribution limited to the northern arid savannas of South Africa (Figure 2). We established a transplant experiment across a latitudinal gradient within the South African savanna biome, inside and outside of the distribution ranges of the species. The latitudinal gradient follows a rainfall gradient. South African savannas also occur across a wide elevation gradient. To take account of both latitude and elevation effects on plant growth, we paired each transplant site across the 850 km latitudinal gradient with a cooler higher elevation savanna site (above 500m.a.s.l). Within each site trees were planted with and without grass competition. As range limits are the spatial reflection of a plant's niche, we predict that across a latitudinal gradient a species will stop occurring where the environmental constraints prevent successful population establishment. Therefore if climate determines range limits we predict the following:

a) In the absence of grass competition, plant performance will decline with increasing distance from the range edge (Hargreaves et al, 2013).
b) In the presence of grass competition, fitness declines will be greater, and performance declines will match current distribution limits, and plants will not establish at sites outside their range.

We also tested an alternative hypothesis, based on the escape hypothesis (Wakeling et al, 2011; Bond et al, 2012), to explain plant distributions across the savanna gradient. We modelled sapling growth based on the maximum growth rates of plants grown with grass and compared the time to reach fire-proof size ('escape height') to the fire frequencies characteristic of each study area. We investigated if the likelihood of plant escape from the fire trap matched current species range limits.

Methods

Eight transplant sites were established within the South African savanna biome across an 850km latitudinal gradient (~8^0 lat.), covering a rainfall gradient from 500mm – 950mm (Table 1). Four low elevation sites (<500 m.a.s.l) were paired with four high elevation sites (>500 m.a.s.l) at the same latitude. With an atmospheric lapse rate of ~5.39°C/1km an increase in 100m in altitude implies a 0.53°C temperature reduction, therefore the higher elevation sites were predicted to be cooler and more prone to winter frost (Schulze, 2007). The latitudinal and altitudinal gradients included sites inside and outside the distribution

ranges of both *C. mopane* and *A. nigrescens* (Figure 1). Sites across these gradients were selected if they occurred within a savanna, had a perennial, undisturbed grass layer and a topsoil clay content of ~25%. At each site, a 30m x 30m plot was established and fenced to prevent herbivory. Each plot was divided into 6 replicates (Figure 2). Three replicates were cleared and the grass cover in the remaining three was preserved. In the cleared treatments grass cover was removed by the roots with a hoe. The treatments were assigned randomly.

A. nigrescens and *C. mopane* seeds collected from a mix of sites across the respective distribution ranges were germinated at a temporary nursery in the lowveld savanna at the South African Wildlife College (-24.453 S, 31.405 E). Seeds were planted in a 1*l* potting bags in a sand: clay mixture. The planting soil was inoculated with soil taken from the roots of each species. Following successful germination, the one month old seedlings were transported to the sites and were planted in the early growing season (3 November – 21 November 2010). Within each replicate five *C. mopane* and five *A. nigrescens* one month old seedlings were planted one metre apart (Figure 3). Seedlings were planted in a random order. As we were explicitly examining the sapling demographic stage and not the early seedling establishment stage, plants were watered for three months following planting. As plant recruitment is pulsed based upon rainfall events, establishment occurs in good years of rainfall. By watering the plants we simulated an early growing season with good rainfall. Plants were provided with 5*l* x 2 per week, the equivalent of a 10mm rainfall event every week.

Measuring seedling survival

Sites were revisited three times annually at the start, middle and end of the growing season (early November, January, April). A round trip between sites was a distance of 5000km; therefore more frequent measurements were not taken. During each measuring period seedling survival was assessed and the standing height and stem diameter of each seedling was measured. At the end of the growing season the grass biomass in the grass treatments was measured using a disc pasture meter (DPM). DPM readings were converted from cm to kg/ha using the conversion developed by Trollope & Potgieter (1986). i-Buttons were placed at each site at 1.2 m above the ground and at 0.15m above the ground to assess the temperature environment the seedlings were experiencing. I-Button data was used to establish the site specific temperatures reported in Table 1. I-Buttons were suspended inside 4mm thick PVC tubes (20cm X 40cm), and remained in the field for the duration of the experiment.

Data analysis

The data were analysed in R. 3.0.0 (R Core Team, 2013). The mean height differences between sites in the last measuring period were analysed using linear-mixed effects models in the nlme package (Pinheiro et al. 2009). The mean annual temperature (MAT) (from i-Buttons) and the mean annual precipitation (MAP) (from the closest SA weather service weather station or farm records) were included as fixed covariates in the analysis. Distribution (inside or outside range) and treatment (grass or no grass) were included as fixed categorical factors. Site was included as a random factor, plot was nested within site. All possible interactions were considered. The model was run and manual backwards model selection was performed. Non-significant terms were removed and the model was rerun until no non-significant terms remained. The different models were compared with an ANOVA and the model with the lowest BIC was selected for each species.

To investigate how the probability of escape from the fire trap influences the distribution of plants we used mean maximum growth rates for the two fastest growing plants of each species from the grass treatment, for each site (Wakeling et al, 2011; Bond et al, 2012). Growth rates were taken from the beginning of the second growing season to the beginning of the third as the growth curve in the first season is characteristic of seedlings which likely have different allocation patterns from established saplings (Higgins et al, 2000). We used the growth model from Higgins et al. (2000) to model the height gain of savanna trees, and hence time to reach a fire proof height (~3m):

——— (Equation 1)

where g_s is the growth rate of stems (cm year^{-1}) (year 2), h_{max} is the maximum stem height (10m), and h_{y-1} is the stem height in the previous year. Starting stem heights were set at a starting height of 20cm, the mean stem height after year one across all the transplant sites. We kept the starting height the same across sites so that responses could be restricted to the sapling stage, not the seedling establishment stage. The model was run for 50 years.

As the model produced an output of tree height per year, we could determine the time it took a tree at each site to reach the fire proof height of 3m, given the maximum growth rate at a site (Wakeling et al, 2012). We plotted this value against the median fire return interval which was estimated by fitting a Weibull distribution (Johnson & Gutsell, 1994) to fire

interval data derived from the MODIS burned area product (see Archibald et al, 2009 for methods) for ~ 1000 points from undisturbed areas across a rainfall gradient.

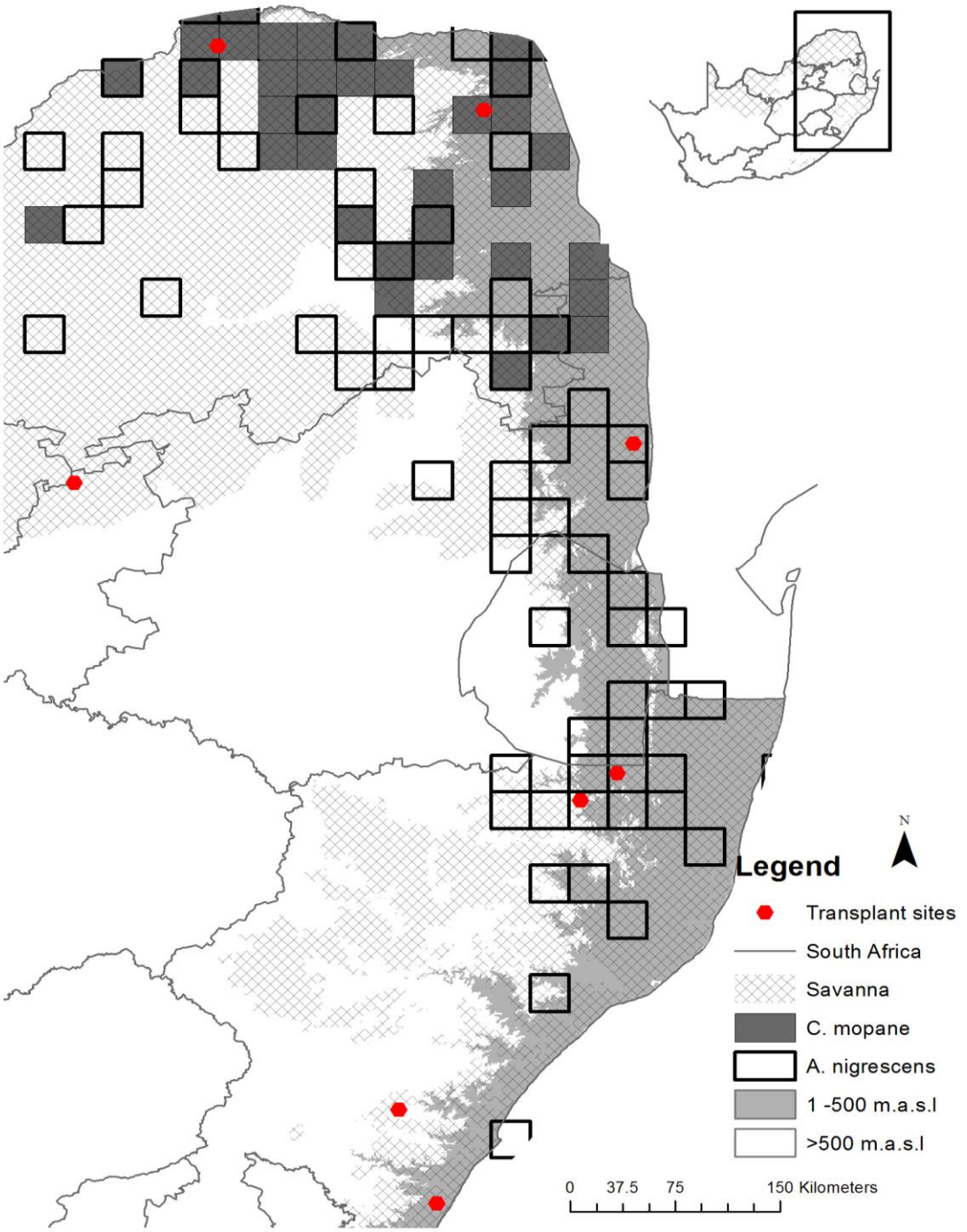

Figure 9: The location of sites across the latitudinal and altitudinal gradient. Four paired sites were placed across a latitudinal gradient. Each site was paired with a higher elevation (white areas) site. The gridded squares indicate the underlying distribution of each of the species planted (*C. mopane* = grey squares & *A. nigrescens* = white squares). All sites were placed within the savanna biome. The northern most sites (~ $22^0$30'S) are referred to as latitude 1 sites and the southernmost sites (~$30^0$30'S) as latitude 4.

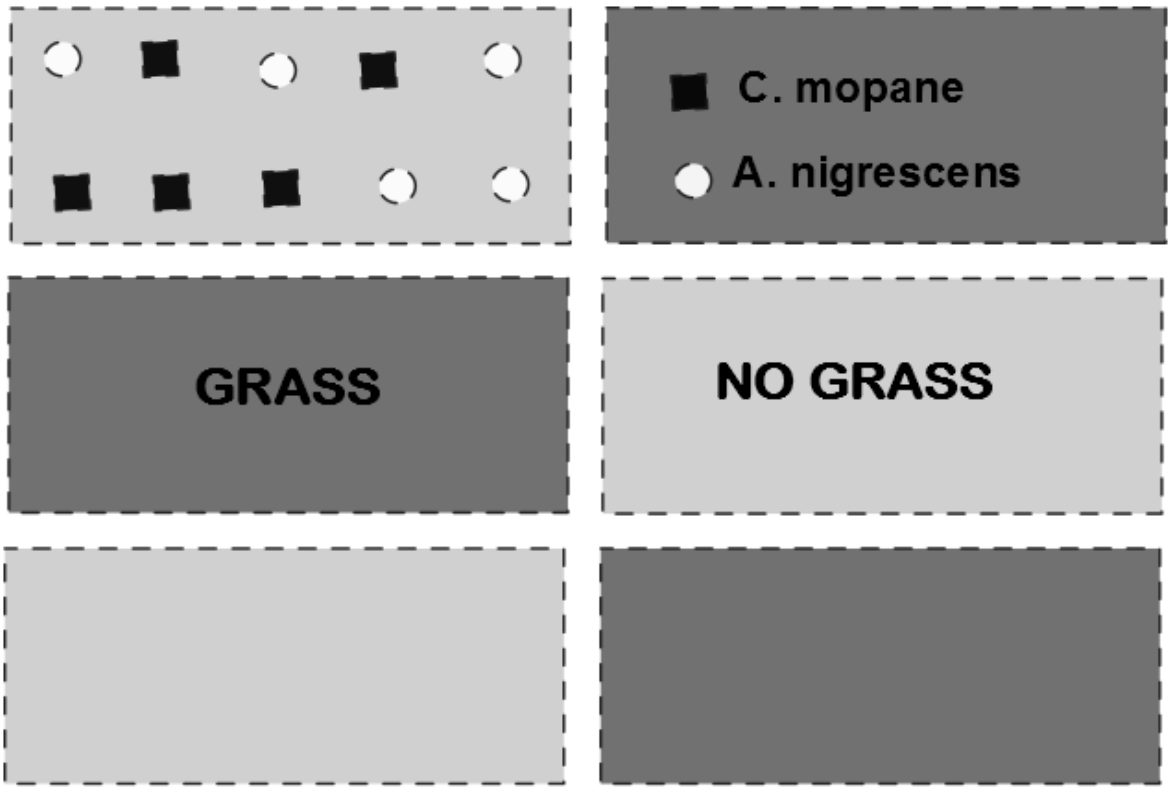

Figure 10: Experimental layout. Each 30m x 30m plot consisted of 6 blocks with three replicates of grassy treatments and three replicates of a cleared treatment, where all grass was removed. Five plants of each species were planted in each replicate, at one metre intervals.

Results

Table 5: Site characteristics. Latitude 1 represents sites at the low latitudes and numbers increase as sites progress southwards.

Site	Latitude	Co-ord's	Altitude	Elev.	MAT*	Mean temp Early wet Season *	Mean temp Late wet season*	Mean temp for 3 coldest months*	Daily mean of coldest day*	No days <13 °C*	MAP mm) **	Grass biomass (kg/ha)	Fire Return Interval confints	*A. nigrescens* distribution	*C. mopane* distribution
PM	1	30.95 E, 22.85 S	Low	427	23.2	25.9	26.8	17.4	9.6	17	532	96	5-6	Inside	Inside
VEN	1	29.25 E, 22.43 S	High	631	24.1	26.2	26.4	17.1	11.9	5	344	120	40	Inside	Inside
LS	2	31.94 E, 25.10 S	Low	197	23.1	25.5	26.3	18.1	12.8	3	625	4056	2.5- 3.5	Inside	Outside
KW	2	28.34 E, 25.39 S	High	1093	19.0	22.4	23.2	12.1	4.8	147	605	626	2.5-3.5	Outside	Outside
TR	3	31.83 E, 27.37 S	Low	221	22.2	23.8	25.7	18.5	12.6	0	748	5437	3-4	Inside	Outside
MAL	3	31.57 E, 27.54 S	High	551	20.9	22.0	24.4	17.2	11.3	4	707	6021	3-4	Inside	Outside
SI	4	30.68 E, 30.3 S	Low	137	20.5	21.1	24.5	16.7	11.8	3	933	9564	3.5-4.5	Outside	Outside
UK	4	30.37 E, 29.63 S	High	850	19.0	19.0	22.3	13.8	7.5	52	840	10728	3.5 -4.5	Outside	Outside

* Temperature values were determined from hourly i-button readings (logger positioned 1.2m high). ** Mean annual precipitation was taken from the nearest rainfall station or from farmers independent records (see Chapter 2: Study site)

Site characteristics

Mean annual precipitation, grass biomass and fire frequency increased as the latitude of the sites increased (Table 1). Mean annual temperatures also decreased slightly with increased latitude, with the exception of the highest elevation site KW (Latitude 2, 1093m) which had the lowest mean annual temperature, and the highest number of cold days. This site was also frosted during winter. The late growing season temperatures of this site are however comparable to the other higher elevation, mid-latitude sites. These trends were similar for both high and low elevation sites. High and low elevation sites differed primarily in their temperatures. Low elevation sites had higher mean annual temperatures and warmer winters than the high elevation sites, with the exception of the Venetia high elevation site, which was the hottest of all the study sites. This site was also the driest of all the transplant sites. Both the northern sites had a very low grass biomass, to the extent that grass fires are unlikely to spread in these areas.

Seedling survival

In the month following planting seedling survival declined sharply (more pronounced for *A. nigrescens*) at all sites. Following this, seedling survival rates stabilised and were fairly constant through the rest of the experiment (Figure 3). The exceptions were the lowest-latitude sites where a constant decline in sapling survival occurred throughout the experiment, except in the warm, no-grass treatment. In latitudes 1-3, seedling survival was always highest in the low elevation cleared sites and lowest in the high elevation, grassy sites. *C. mopane* seedling/sapling survival over time was lower in its distribution range than outside the distribution range (Figure 3).

Mean height over time

The patterns of plant growth did not meet our expectations as plant height did not decline as expected with increasing distance from either species range edge (Figure 4 &5), nor with a climatic gradient. Rather, at some sites, in the absence of grass, plant growth was greater outside than inside the distribution range (Figure 4 & 5). Mixed linear models showed that neither the climatic factors (temperature and rainfall), nor distribution range alone could explain patterns of growth for *C. mopane* and *A. nigrescens* (Table 2). The presence of grass in the grass treatment for both species was the most important single factor that explained plant performance, with the presence of grass reducing tree growth (Figure 4 & 5). The

model that best explained the final season height measurements for *C. mopane*, across a temperature and rainfall gradient, consisted of treatment (grass v. no grass), the interaction of grass treatment and distribution range and the interaction of grass treatment and rainfall (Table 2). In the presence of grass, *C. mopane* was always shorter, except within the distribution range where the effect of grass treatment was negligible due to the very low grass biomass at the sites. Grass treatment x rainfall interaction presumably was due to the increased grass biomass with high rainfall. Similarly *A. nigrescens* growth was best explained by grass treatment alone (Table 2).

Table 2: Mixed linear model outputs showing the best model selected using BIC values for *C. mopane* and *A. nigrescens.* Bold terms indicate significance. Treatment was with or without grass, distribution was either inside or outside the plant range and MAP is precipitation at a site.

	C. mopane				*A. nigrescens*			
	numDF	denDF	F-value	p-value	numDF	denDF	F-value	p-value
Intercept	1	87	9.04	**0.004**	1	87	12.95	**<.0001**
Treatment	1	33	34.97	**<.0001**	1	35	29.57	**<.0001**
Treatment: distribution	1	33	3.19	**0.084**				
Treatment: MAP	1	33	0.71	0.4				

KW (latitude 2, high elevation) was the only site which experienced frost. During the dry season in year 1 there were several severe frosts which caused a decline in height for both species, as can be observed by the big decrease in mean height between season 3 and 4 (Figure 4 & 5). Frosted trees of both species were topkilled, but both species resprouted from the base in the following growing season. Resprouts were always multistemmed (Figure 6).

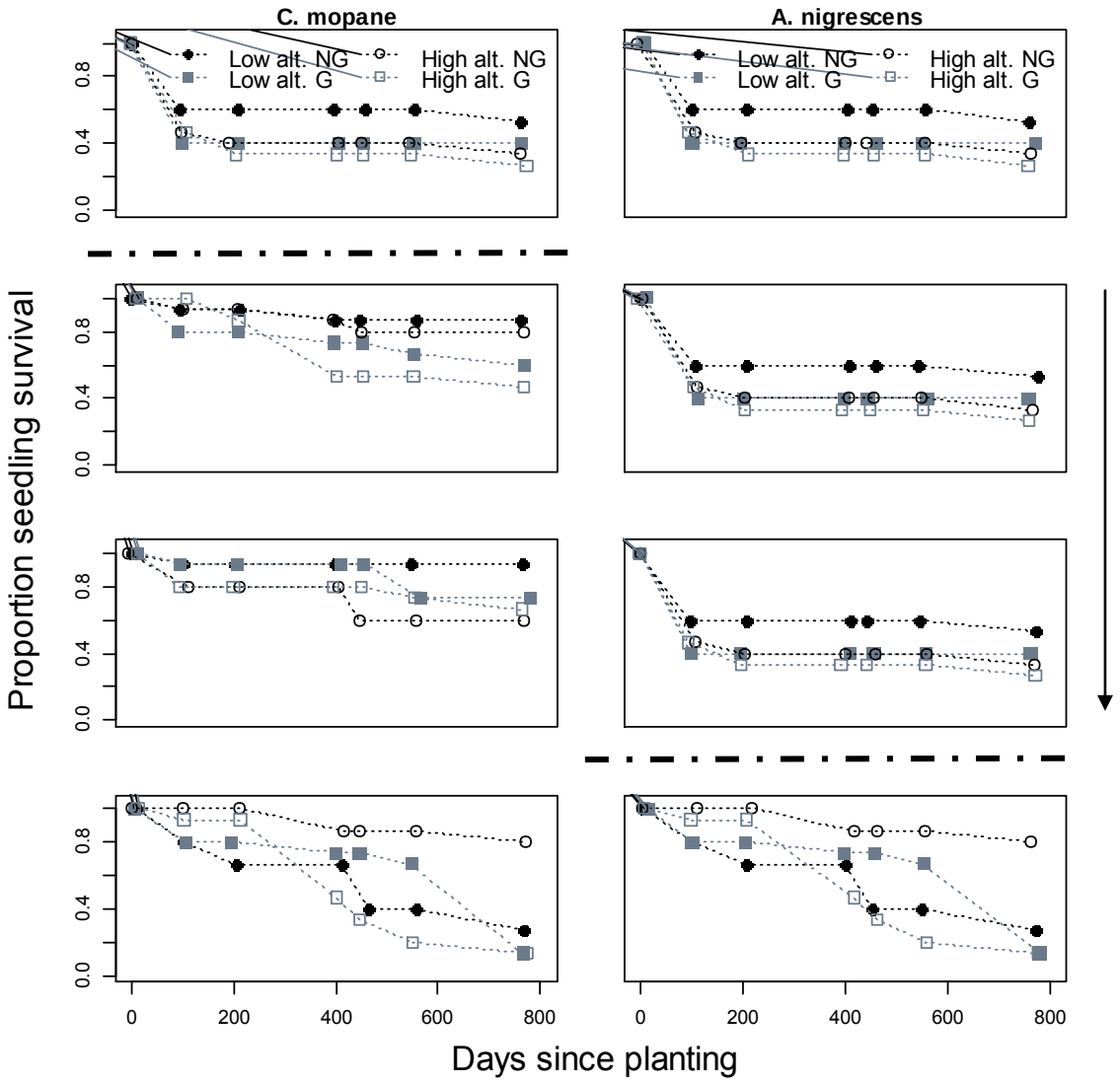

Figure 3: The proportion of seedlings surviving in transplant experiments across a latitudinal (top, northerly, to bottom, southerly) and elevation gradient. Most sites showed a rapid decline in survival after planting after which survival rates stabilised. The exceptions were the highest-latitude sites (most southerly) that showed a constant decline in sapling survival throughout the experiment in all cases except the warm, no-grass treatment. Open points indicate higher elevation sites and the shaded points represent the low elevation sites. NG = No grass treatment, G = grass treatment. The dashed line represents the location of the species distribution limit in each instance.

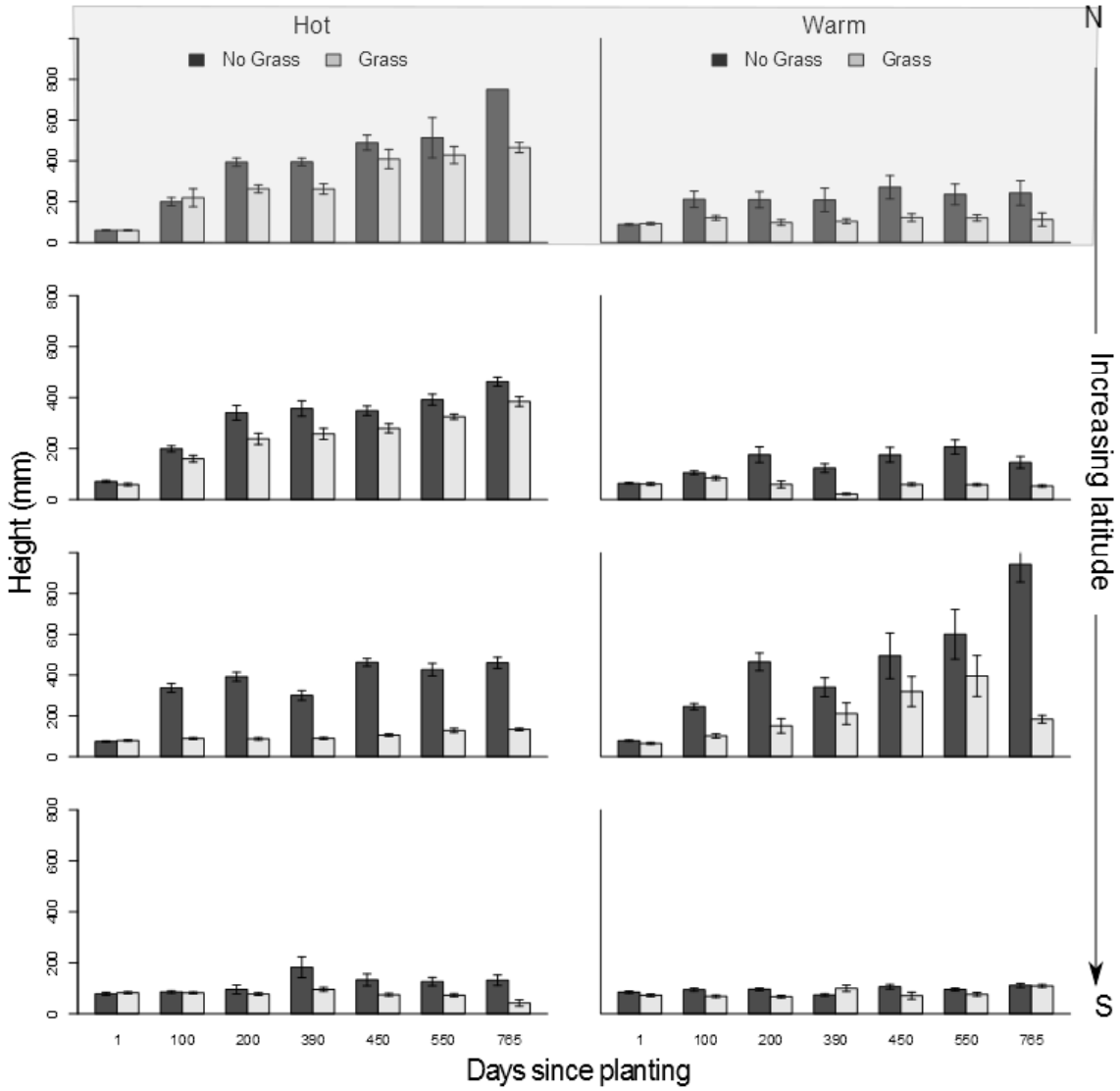

Figure 11: Mean growth patterns over time for *C. mopane* across a latitudinal gradient (top, N, to bottom, S) with matched low (left) and high (right) elevation sites. The bars show the mean height for each measuring interval and the whiskers indicate standard error. Growth measurements were taken at the beginning, middle and end of the growing season, thus measurements are for two growing seasons, and the beginning of the third. Mean height often declined following the non-growing dry season. Shaded graphs indicate a site which is within the distribution range.

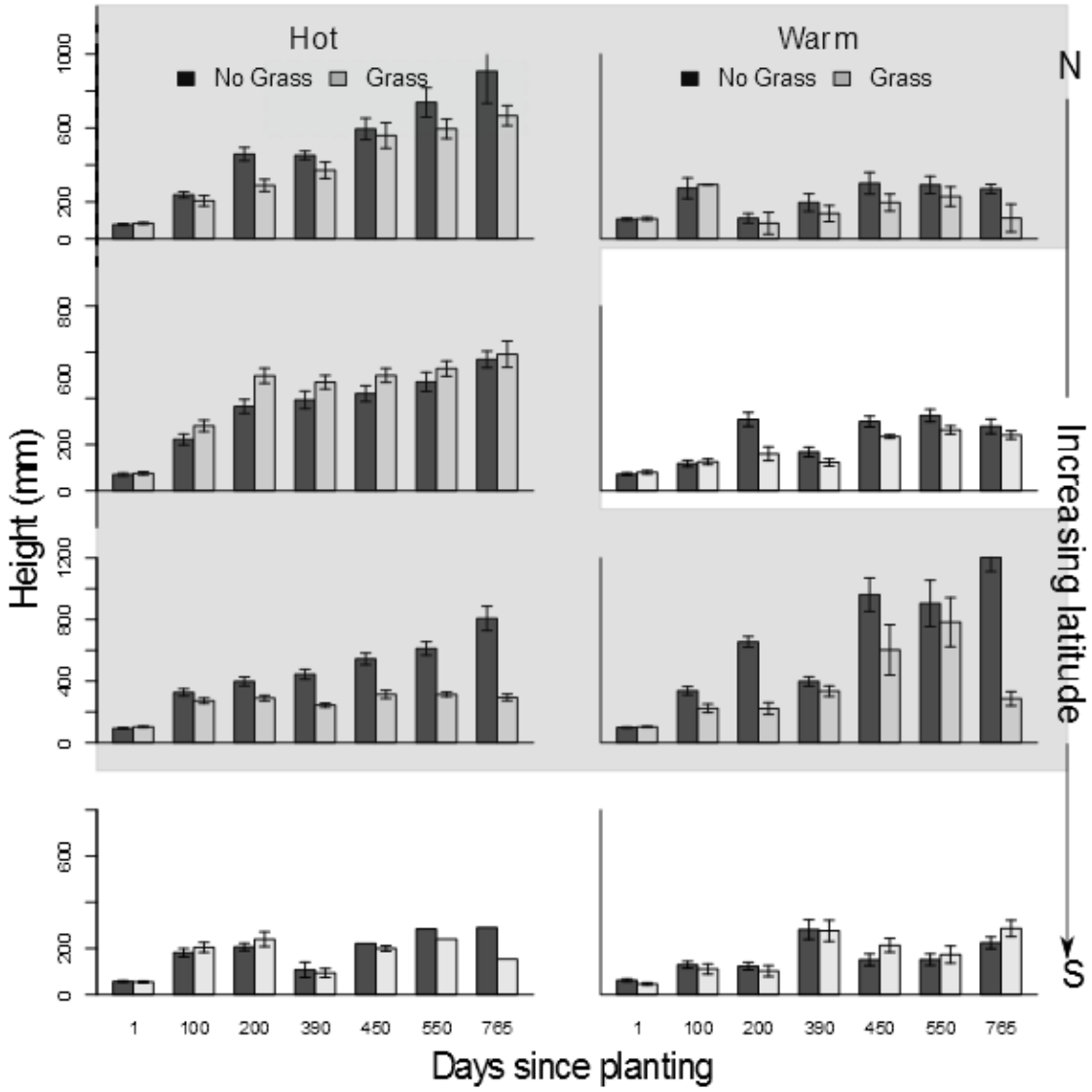

Figure 12: Mean growth patterns over time for *A. nigrescens* across a latitudinal gradient (top, N, to bottom, S) with matched low (left) and high (right) elevation sites. The bars show the mean height for each measuring interval and the whiskers indicate standard errors. Growth measurements were taken at the beginning, middle and end of the growing season, thus measurements are for two growing seasons, and the beginning of the third. Mean height often declines following the non-growing dry season. Shaded graphs indicate that the site is within the distribution range.

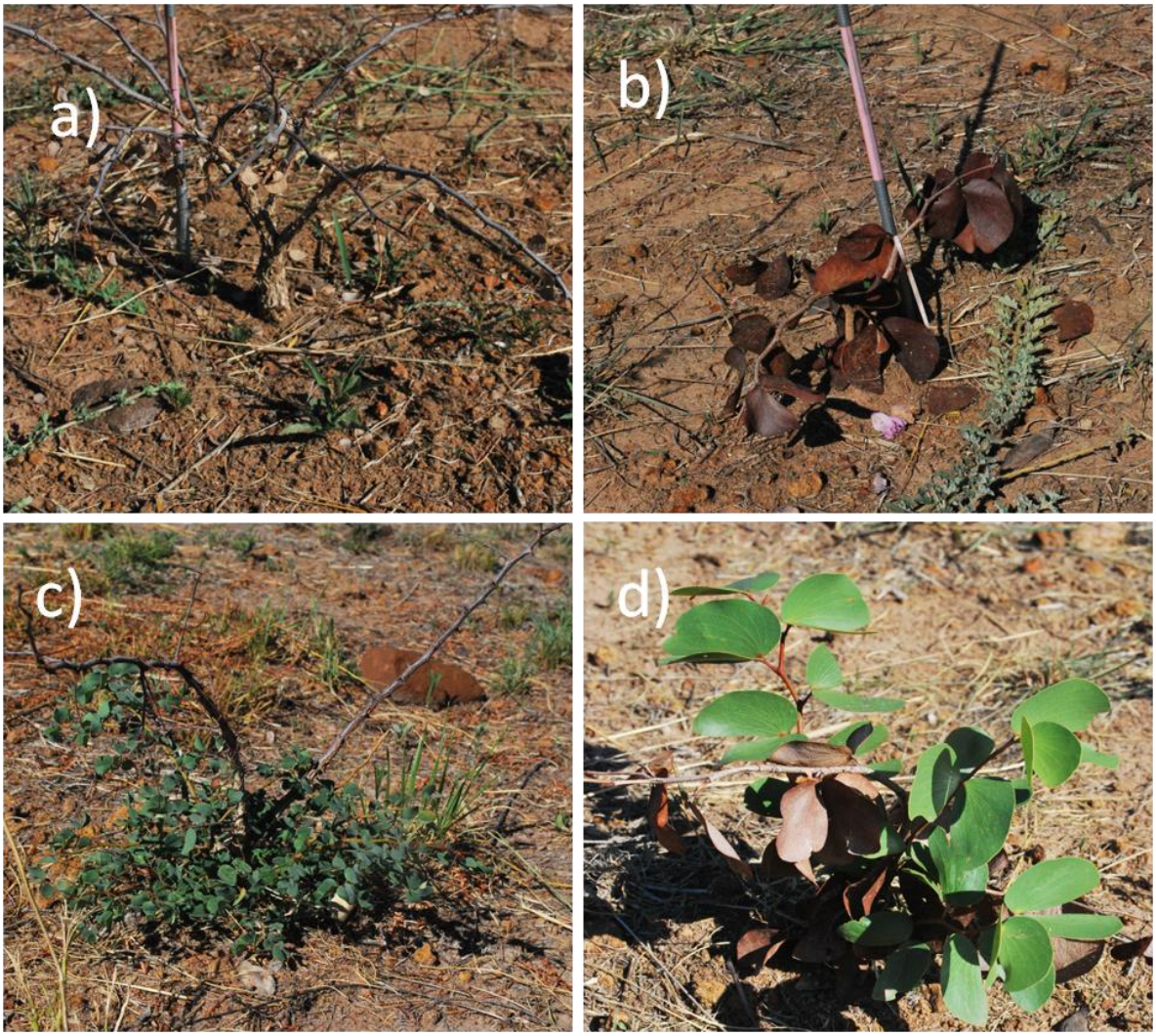

Figure 13: Frost induced top kill at the coldest site (KW) of a) *A. nigrescens* (out of range) and *b*) *C. mopane* (out of range). In the following growing season both species (c) *A. nigrescens* and d) *C. mopane* responded to frost by resprouting multiple stems from the base

Maximum plant growth

As the clearest factor affecting plant performance was the presence of grass (Table 2) we examined this relationship further. At each site we examined the variation of plant heights in the grass treatment in the last measuring period (Figure 6 & 7). There was a high variation in plant height between the sites. In the low elevation sites the maximum plant height of all the sites occurred in the distribution range of *C. mopane.* It then declined with increasing latitude. This pattern was less clear in the higher elevation sites. Similarly for *A. nigrescens,* the maximum plant height at each site was highest inside the distribution range of the low elevation sites. Again this pattern was not repeated in the higher elevation sites.

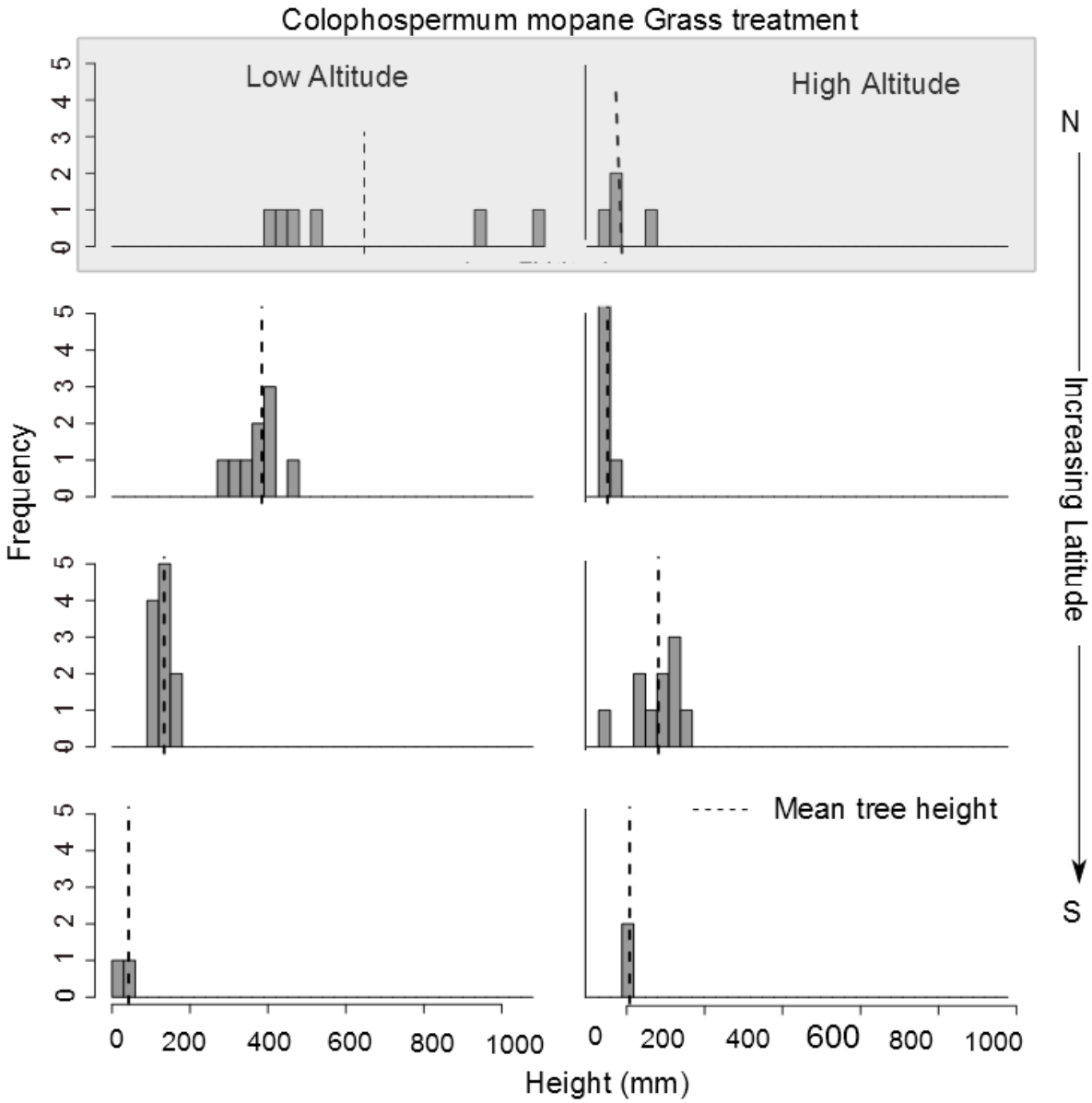

Figure 14: Frequency distribution of *C. mopane* tree height in grass treatments for the last growing season. Shaded graphs indicate that the site is within the distribution range. Dashed line indicates

mean tree height for the grass treatment for each site

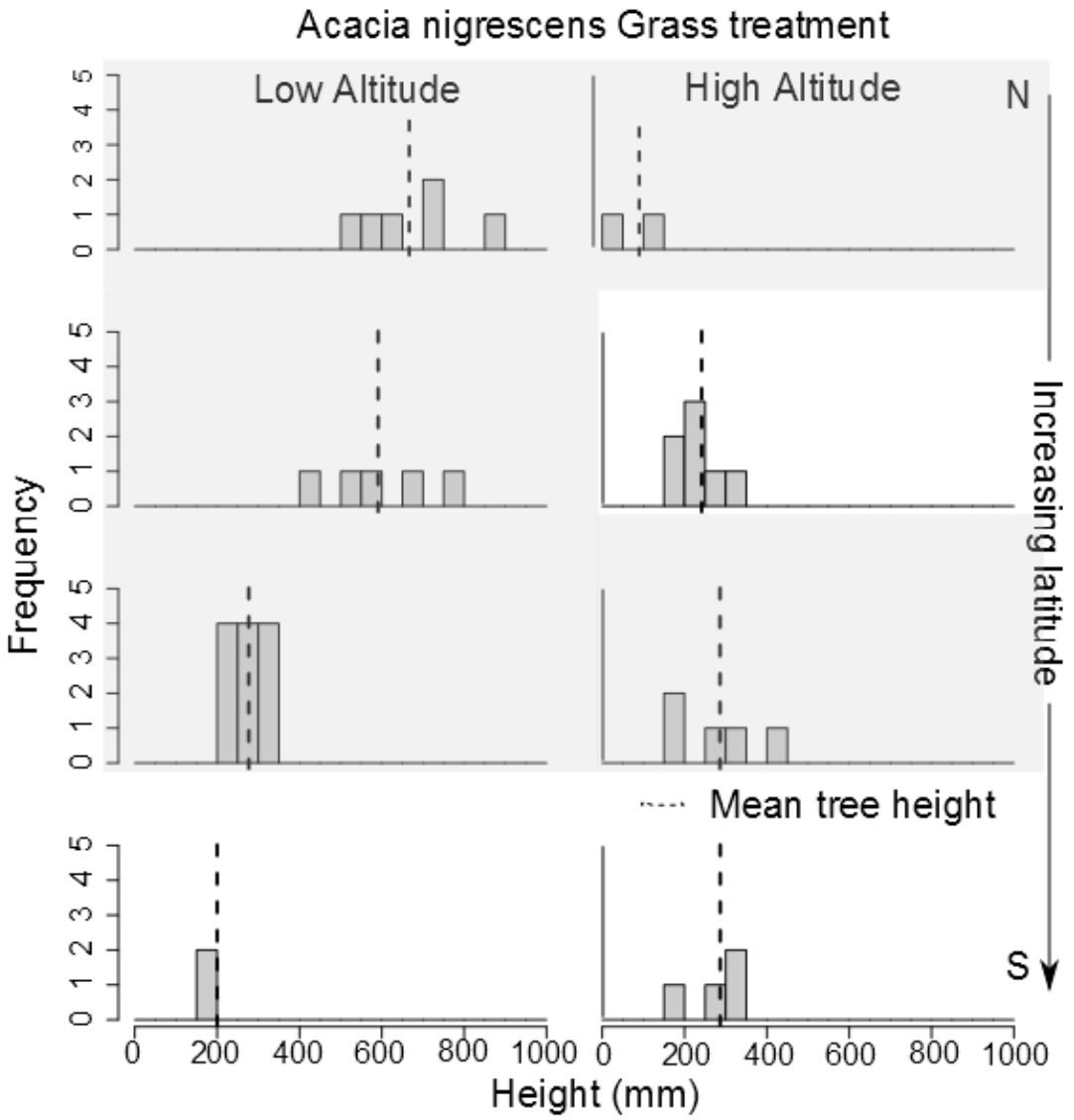

Figure 15: Frequency distribution of *A. nigrescens* tree height in grass treatments for each site in the last growing season in the grass treatments. Shaded graphs indicate that the site is within the distribution range. Dashed line indicates mean tree height for the grass treatment for each site

Modelled tree growth and escape from the fire trap

The probability of sapling escape from the fire trap is a good indicator of whether a species will be present at a site (Figure 9). Plants which were planted inside their distribution ranges were more likely to reach fire escape height within the fire free interval common to their area. *C. mopane* fails to escape from the fire trap when maximum growth rates are low (caused by high grass biomass) (Figure 7 & 8), or fire return interval is short (Table 1). The species is

common only in areas where the fire return intervals are in the order of decades or the grass biomass is low (Table 1). *A. nigrescens* has a better ability to maintain higher maximum growth rates in the presence of grass when compared to *C. mopane.* The estimated escape probabilities decline for *A.nigrescens* when it is grown in high rainfall areas where grass biomass is high (Figure 9).

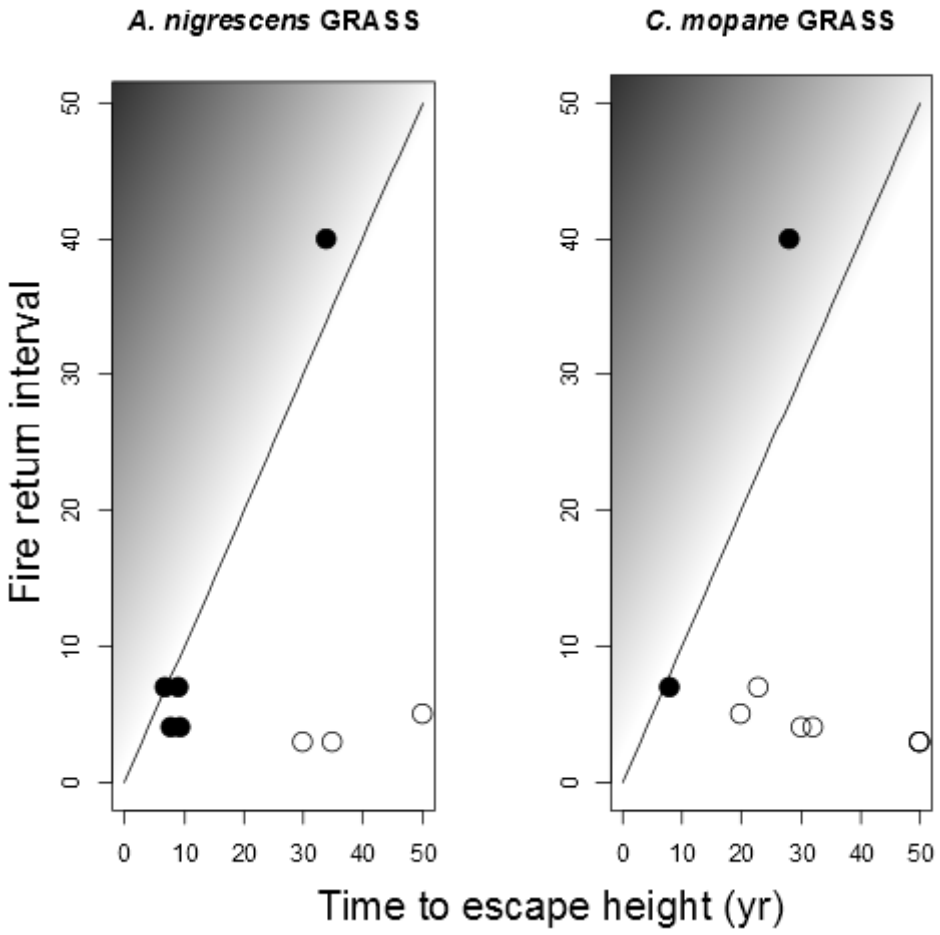

Figure 16: The modelled time to reach escape height in the presence of grass plotted against the approximate fire return period for the site. Closed circles show a species was planted within its distribution range, open circles show the plant was grown outside its distribution range. The solid diagonal line indicates the minimum fire return interval required for each time-to-escape-height value. If the points fall above the 1:1 line, into the shaded area, the plants have a high probability of escaping from the fire trap. Both species, if planted within their distribution range, have a reasonable probability of escaping the fire trap. Estimated growth rates are too slow for saplings to escape the prevailing fire regimes outside their distribution range.

Discussion

Neither study species demonstrated predictable declines of seedling survival or mean plant growth with increasing distance from their range edge or with climate. Grass competition had a significant effect on the plant performance across all sites, although grasses did not completely exclude a tree from a site across either latitudinal or altitudinal gradients. The study species distribution limits were best explained by the ability of a sapling to escape from the fire trap which was set by a combination of the maximum sapling growth rate in the presence of grass and the mean fire return interval for a given site. In the drier sites low grass competition coupled with a long fire return interval allowed trees to escape from the fire trap. When sites got wetter grass competition was high and fire return intervals were short. This selection filter determined which plants could occur survive in an area.

As the plants survived and grew across both latitudinal and altitudinal gradients, a classic interpretation of the results would be that both these species were dispersal limited as suitable but unoccupied areas existed beyond their range boundaries (Hargreves et al, 2014). While dispersal limitation certainly occurs, it is not a common occurrence (Sexton 2009, Hargreves 2014), and it is highly unlikely that these two widely spread, common savanna species are dispersal limited. Although Madams, (1990) has suggested that this is true for *C .mopane*, its fruits are well dispersed by wind and water (Styles and Skinner 1997, Mlambo & Nyathi, 2001), and allozyme frequencies are similar across Southern African populations, indicating that an effective mechanism of gene flow occurs (Villoen et al, 2003). The dispersal strategy of *A. nigrescens* is less well understood (Midgley & Bond, 2001), but the closed pods remain on the tree until ripe, when winds, associated with the onset of rains, rip the pods off the tree where they open, scattering the seeds widely (Miller, 1994; Grant & Thomas, 2001).

The main climate variables, temperature and precipitation, did not directly predict plant presence nor performance across either the latitudinal or altitudinal gradient. Although this finding is contrary to expectations that seedling survival and plant above ground biomass will increase with higher soil resource availability (i.e. water and nutrients), other studies in South African savannas also indicate that manipulations of rainfall intensity and soil nutrient status neither increase the survival rate of savanna seedlings (Barbosa et al, 2014a; Barbosa et al, 2014b), nor increase tree growth (February et al, 2013; Barbosa et al, 2014b). Instead, in our study, the presence of grasses had the strongest effect on sapling performance by suppressing tree growth. At this demographic stage, the competitive interaction between trees and grasses

is likely to be highest as tree and grass roots occupy the same soil depth (Cramer et al. 2007). Whilst herbaceous competition does strongly suppresses sapling and tree growth (Cramer et al. 2007, 2009; Riginos, 2009; van der Waal et al, 2009), through competition for light and nutrients (Cramer et al, 2007; 2009; van der Waal et al, 2009), it does not prevent trees from surviving at a site. In our study rainfall had an interaction with grass treatment, where increased rainfall increased grass biomass (O'Connor et al, 2001). Savanna trees, growing in the presence of grass, often do not benefit from increases in resource conditions (e.g. increased water addition) as herbaceous competition is intensified (Sankaran et al. 2008; van der Waal et al. 2009; February et al. 2013; Barbosa et al, 2014). Although grass competition did not prevent a tree from growing at a site, and therefore could not directly limit species distributions, the suppressed sapling growth in the presence of grass affected the probability of escape from the fire trap (Higgins et al, 2000; Wakeling et al, 2012). Successful sapling escape therefore depended on a combination of maximum tree growth rates and the length of the fire free interval (Figure 9). Abiotic and biotic factors that affect either the maximum plant growth rates or fire frequency (e.g. Archibald et al, 2010) can be important indirect drivers of plant distribution but the direct control is the interaction between growth rates and disturbance frequency.

Frost is one climatic factor that is often considered to be important in limiting tree distribution, particularly *C. mopane* (Henning & White, 1974; O' Connor & Bredenkamp, 1997; Sebego 1999 (and references therein); Okitsu, 2005; Burke 2006). We demonstrated that at the coldest site (Kwalata, latitude 2) both species survived severe frost (Figure 6), and multiple shoots resprouted from the base in the following growing season. While frost is unlikely to directly limit the occurrence of savanna plants (Brando & Durigan, 2004; Holdo, 2005, Wakeling et al, 2012; Whitecross et al, 2012) it can have important indirect effects on plants by increasing the time for a plant to reach fire proof sizes (~3m). As frost can cause topkill (especially in < 2m trees), it can be seen as similar to fire in keeping plants reproductively immature and exposed to further frost and fire disturbances (Holdo, 2005; Whitecross et al, 2012) suggesting that in conjunction with other disturbances it can also be an important indirect limitation on species distributions (Holdo, 2005, 2007; Whitecross, et al, 2012).

C. mopane could only obtain high maximum growth rates, and successfully establish when grass biomass was absent or very low. In the northern most sites which were in its

distribution range, the fire return interval is high, and given the biomass at the PM site (low elevation, latitude 1), the fire return interval should be even higher than that estimated from our method. Above 4000kg/ha grass fires spread easily, but the likelihood of fire spread rapidly declines to a minimum threshold fuel load for fire spread a little below 2000kg/ha (Trollope et al, 2002). Although the local site conditions at the PM site caused a lower grass biomass than predicted by climate, the growth rates and the calculated fire regime still produced conditions suitable for escape from the fire trap. As grass biomass increased, the *C. mopane* maximum growth rates decreased and its ability to reach fire proof height (~3m) in the fire free interval declined. Its current distribution is characterised by dry areas with a low grass biomass, caused by both low rainfall and the tendency of *C. mopane* to competitively exclude grass (Smit & Retham, 2000; Ward 2012). *C. mopane* has low fire induced mortality (van Wyk & Fairall 1969; Ben-Shahar, 1996) and resprouts vigorously following top kill (Mlambo & Mapaure, 2006) and is therefore considered fire tolerant. However in response to top kill it resprouts multiple stems from the base and seldom regains its single stemmed stature. The shorter, multi-stemmed shrub form (Mlambo & Mapaure, 2006, Kennedy & Potgieter, 2003; Higgins et al, 2007), if retained permanently, all but prevents future escape from the fire trap. As *C. mopane* trees below two meters in height do not produce seeds (Caughley, 1976; *pers obs.*) these trees are effectively sterile. *A. nigrescens* occurs in semi-arid savannas, and our results show that within this range they can escape the fire trap in the presence of grass. *A. nigrescens* is a nitrogen fixing legume (Cramer et al, 2007; 2009). Whilst N fixing plants do not necessarily always fix nitrogen, *A. nigrescens* saplings increase N fixation when grown in competition with grass. This adaptation improves *A. nigrescens* growth in the presence of grass competition. However in the wetter (highest grass biomass) and frosted sites their growth rates were too slow to escape the fire trap. *A. nigrescens* saplings possess more traits to overcome a herbivore imposed sapling bottleneck than a fire imposed bottleneck (Forna & Du Toit, 2007; Staver et al, 2012) so that this species is unable to establish in a strongly fire dominated system (Staver et al, 2012) as it has a poor ability to grow where grass productivity is very high, or where fires are too frequent to reach fire-proof sizes in the inter-fire interval.

Neither fire nor grass competition alone can explain the distribution limit of these two species. Both are known to resprout vigorously after fire, and our experiment shows that while saplings show reduced growth rates with grass, they were not excluded. It is the combination of these two factors – combined with the fact that savanna trees are not

reproductively active until they have grown tall, that can explain the distribution patterns we see. The interactive role of fire and resource constraints on potentially determining the distribution of species has not been widely considered before. Fire is an important top-down control and its importance in physically structuring woody plants, limiting tree recruitment and plant density is widely recognised (e.g. Higgins et al, 2000; Hoffmann & Solbrig, 2003; Smit et al, 2011; Werner & Franklin, 2011). While it is also acknowledged that the prevailing fire regime of an area can alter species composition at a local scale, (Trapnell, 1959; Jose & Farinas, 1983; Hoffman et al, 2004; Bond et al, 2012) it has not been explicitly considered to be a process that can shape the regional distribution of species. Our results show that top-down processes are important in explaining the distribution of these two savanna tree species. Top-down controls like fire and herbivory can act as strong environmental filters and thus be as important in shaping plant distributions as temperature in temperate systems. This is an area of research that urgently requires more attention in savannas as fire and herbivory can be managed far more than global temperature change allowing greater regional control on changes in species distribution limits.

Conclusions

Our results reveal that climate does not directly determine the distribution of two savanna tree species, but highlights how a combination of biotic control (competition with grass) and the prevailing fire return intervals can explain distribution limits of these trees.We demonstrate that the climate based framework for predicting species distribution is not appropriate to describe savanna plant distribution or for climates where "ecosystems are uncertain". Top-down controls like fire and herbivory are likely to be very important environmental filters for many savanna trees and although some savanna species distributions may relate to climate e.g. rainfall (through controls on grass productivity), the direct underlying mechanism driving their distribution is not climate. Predicting future changes in response to climate change is therefore not straight forward and requires further study

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Chapter 6: Irrigation delays leaf drop in an arid savanna woody plant

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NS, SA, AN, conceived the original experiment, which was abandoned and NS designed the current experiment using the previous experimental setup, NS,SA, AN conducted the field work; NS performed the analysis and built the leaf carbon model;, AS donated phenology data, NS wrote the manuscript, SA had a supervisory role and commented on the manuscript, RS, SA funded the project.

Abstract

Seasonal patterns of leaf display dictate the time available for resource capture in plants, therefore understanding the environmental cues that drive leaf phenology enable us to predict drivers of a plant's current and future distribution ranges. In savannas, as water availability is the primary driver of productivity, we investigated if soil moisture is a proximal cue for leaf fall in the deciduous mono-dominant *Colophospermum mopane* using an irrigation experiment. We tracked the leaf carbon balance into the dry season in both irrigated and control plants to investigate if leaf drop was a function of reduced leaf carbon assimilation driven by changing water availability or a function of leaf age.

Water is a proximate cue in driving leaf loss of mopane. Leaf carbon acquisition rates do not decline through leaf aging, but are strongly affected by soil moisture availability and temperature. Leaf loss does not occur when leaf C gain is zero, nor when a particular leaf carbon threshold is reached. Non-irrigated plants retained their leaves late into the dry season and still remained photosynthetically active, a feature that may contribute to the numerical dominance of this species. Our findings highlight the need to understand the costs and benefits of facultative deciduousity, and obligate deciduousity before we can explain the range and causes of different phenological strategies in savannas.

Introduction

Seasonal patterns of leaf display dictate the time available for resource capture in plants (Chuine 2010). These patterns in turn affect a range of ecosystem functions and can determine competitive interactions, evapo-transpiration and nutrient cycling rates and limit browser population densities (Langvatn *et al.* 1996; Scholes and Archer 1997; White et al. 1999; Owen-Smith and Ogutu 2003; Penuelas et al. 2009; Korner and Basler 2010; Polgar and Primack 2011). Climate change can alter the timing of such phenological events (Parmesan 2006), with the extent of the change varying among species depending on their phenological plasticity. A high level of plasticity ensures plants are capable of adjusting their phenology to the available resources and climate (Givnish 2002; Oikawa et al. 2006; Chuine 2010). These species are more likely to adapt to changing climates and to persist in areas with novel climates. Greater plasticity is expected where phenology is dictated by climate-related cues (Borchert, 1994; Chuine, 2010). Species where phenology is determined by non-variable environmental cues (e.g. photoperiod) and genetics (e.g. a set leaf age), will be less able to adjust to new conditions and may be competitively disadvantaged (Korner and Basler

2010). Determining the factors controlling leaf phenology, particularly in systems which have previously been little-studies, such as savannas, will improve our ability to predict future species distributions and potential ecosystem consequences of altered phenology.

African savannas are dominated by deciduous trees, with deciduousity thought to be an adaptation to the characteristic long dry season in this biome and, more generally, to strong seasonal variation in climatic variables (Kikuzawa 1991; Shackleton 1999; Givnish 2002). In temperate systems, temperature and day length are the major environmental cues of leaf display and fall (Chuine and Cour 1999; Jolly et al. 2005; Polgar and Primack 2011). The seasonality in tropical savannas is related to water availability, rather than temperature, so there is reason to believe that the cues for leaf drop will be different (Harrington 1991). Water availability is therefore a likely critical cue in initiating the timing of leaf display and drop (Borchert 1994).This idea is not widely supported by irrigation experiments in water limited, dry tropical forests (Wright and Cornejo 1990; Myers et al. 1998). The variability and asynchrony of leaf drop found in savannas (Archibald and Scholes 2007; Higgins et al. 2011) with the arrival of the dry season suggests either a) water availability is the main cue driving leaf fall, but it manifests itself differently in different species, or b) only some species are responding to water stress, while others have leaf drop cues which are not linked to the main driver of productivity in the system. Declining photoperiod (Borchert 2002), leaf age (Reich et al. 2009), vapour pressure deficit (VPD) (Do et al. 2005) and temperature (Specht 1984) have been highlighted as potential alternative cues that initiate leaf drop. Correlative studies suggest that day length and/or temperature could be important cues in savanna systems (Archibald and Scholes. 2007). Alternatively, deciduousness might simply be determined by photoperiod or maybe genetically set in some species.

In response to a proximate environmental cue leaf drop occurs. A likely ultimate physiological explanation of leaf drop is changing carbon balance of a plant over the seasons. The carbon balance hypothesis proposes that leaf drop occurs when carbon costs exceed gains (Chabot & Hicks, 1982; Vincent, 2006; Reich et al, 2009). Some authors propose that leaves are dropped when the daily net leaf carbon balance is zero (Oikawa et al, 2006; Reich et al, 2009). Alternative variations, based upon whole plant C gain, suggest leaves are shed when the daily leaf carbon gain cannot offset the root and stem respiratory costs of the whole plant (Givnish, 2002; Reich et al, 2009). A small set of environmental variables are important in setting leaf carbon status (water, light, temperature), (Nobel, 1984; Scheiter &

Higgins 2009; Higgins et al, 2012). Leaf age, an important factor in deciduous species, is also frequently considered to contribute to leaf carbon decline. After a leaf is fully expanded its photosynthetic rate generally experiences a monotonic decline (Sestak et al 1985), which has been attributed to increased self shading (Reich et al, 2009; Kikuzawa, 1995), to redistribution of resources to younger leaves (Kitajima et al, 1997) and to cumulative tissue deterioration and aging (Reich et al, 2009; Oikawa et al, 2006). However not all trees demonstrate this relationship with leaf age. Prior et al (1997) demonstrated a seasonal photosynthetic trend, independent of leaf age where photosynthetic rates declined in response to environmental variables (increasing soil and atmospheric dryness), recovering the following wet season. Another hypothesis, relevant to water limited savanna systems, is that water availability acts not only as a proximate cue but also as an ultimate cause of leaf drop. Leaf shedding is driven directly by decreasing water availability, where leaves are dropped to prevent water loss through transpiration, this can occur before leaf carbon reaches zero (Chabot & Hicks, 1982; Reich and Borchert 1984; Tyree et al, 1993; Borchert 1994; Kutsch, et al, 2009).

In South African savannas with highly seasonal rainfall, we were interested to determine whether leaf drop in a dominant deciduous tree is a function of reduced carbon assimilation initiated by a proximate cue or whether leaf drop is hard-wired in the sense that leaves are dropped when they reach a certain age threshold, even when sufficient resources are available. As the drivers of leafing out in savannas have received more attention than those of leaf drop, we investigated leaf abscission in the tropical monodominant savanna species *Colophospermum mopane* (mopane) (Kirk ex Benth.) Kirk ex J.Léon. We selected *C. mopane* as it is a tropical monodominant species which almost singly dominates 25-35% of southern African savannas (Mapaure, 1994; Timberlake, 1995). It occurs at the arid end of the spectrum of savannas and thus experiences a strongly seasonal environment with long dry seasons. Unlike many co-occurring arid species which drop their leaves early in the dry season, *C. mopane* maintains its leaves late into the dry season shedding most of its leaves only in August (Hooimeyer 2005, Potgieter and Wessels 1998, Dekker and Smit 1996). According to some climate change scenarios, the species will extend its extensive current distribution southwards and westwards (Rutherford *et al.* 1999). Given its atypical ecology and potential vulnerability to climate change impacts, understanding the proximate phenological cues and the corresponding plant response thereafter is important. We aim to determine if soil moisture is a proximate cue for leaf fall in *C. mopane*. Using an irrigation

experiment, we investigated if leaf fall can be altered by manipulating soil moisture availability. Additionally we tracked the leaf carbon balance into the dry season in both watered and un-watered plants. In so doing we aimed to determine if leaf drop was a function of reduced leaf carbon assimilation or simply a function of leaf age. We investigated if leaf fall is consistent with the leaf carbon balance hypothesis and occurs when the individual leaf carbon balances are zero.

Methods

Site

The watering experiment was set up at Phalaborwa Gate in the Kruger National Park (~ $31^0$23'12E, $24^0$22'3S). This area is characterized by hot, wet summers and cool, dry winters (mean annual temperature of 23.1 °C with a mean max temperature of 31.7 °C in January in mid-summer and a mean minimum temperature of 9.6 °C in July; mean annual rainfall of 481 mm) (South African Weather Service, Phalaborwa station)). The area is underlain by granite/gneiss parent material and consists of moderately undulating hills (Gertenbach, 1983; Venter *et al.* 2003) with a granitic catenal sequence: sandy soils on the crests and clayey soils along the footslopes (Scholes & Walker, 1993; Venter *et al.*, 2003). Woody vegetation is dominated by *Colophospermum mopane* interspersed with *Combretum apiculatum* (Gertenbach, 1983). Six large adult trees (>3m tall) positioned on a flat area along the catenal crest were selected and tagged for measurements between April 2010 – Jan 2011. Three trees received a watering treatment and three trees were left unwatered. Watered trees were each irrigated for 2 hours every second week, using a hosepipe (Fig 1). Control trees could receive water from any natural precipitation events, but were subject to the natural drying down process. The experiment was initiated at the beginning of April at the onset of the dry season; thereafter field campaigns took place in May, June, July, August, November, and January 2012. Watering was stopped in late August 2012 towards the end of the dry season.

Tree response measurements

One hour prior to dawn two fully grown, healthy green leaves were picked from every tree. Predawn leaf water potentials were measured on these leaves, using a Scholander pressure device. Predawn measurements were made in all the dry season field campaigns; April, June, July and August 2011.

As a measure of canopy fullness, the canopy light interception of each individual tree was recorded using a ceptometer (Decagon) at 10am every field campaign except in May. Leaf health was recorded from the May field campaign. Two large tree branches were selected and marked on every tree in the experiment to track leaf health changes over time. Every leaf was tagged on the branch using different coloured cable ties. The colour was assigned according to a leaf health index: 1) leaf was 100% green and not fully grown, 2) Leaf was fully expanded and 100% green, 3) leaf was healthy and 95% green but had small black spots, 4) leaf was less than 60% brown 5) leaf was more than 60% brown. Every following campaign the number of leaves in each category were counted and relabeled according to their new categorisation.

During each campaign gas exchange measurements were taken on the same two marked leaves at 8.00, 10.00, 12.00, 14.00 and 16.00, using a LI-COR 6400 XT mounted on a tripod. Incoming air was passed through silica desiccant and humidity remained between 22-24%. These measurements were taken under constant light (PAR = 1500 µmol m^{-2} s^{-1}, temperature (25°C) and flow rate (500 mmol s^{-1}) to control for short-term changes in environmental variables and ensure that changes in plant status would be driving differences between dates. Light response curves were also performed for both treatments during each campaign. Leaves were measured on clear cloudless days.

Chlorophyll fluorescence measurements were performed on two leaves of each age category on every tree. Leaves were pre-darkened for 20minutes. Maximimal PSII photochemical efficiency (Fv/Fm) was determined for each leaf.

Community phenology

The phenology of the surrounding *C. mopane* community was recorded for the entire 2011. Every two weeks, ~40 trees across the landscape were assessed according to their phenology, as per Archibald & Scholes (2007). Trees were classified according to the number of green leaves in the canopy: 0 (no green leaves), 1 (less than 10% green leaves), 2 (20-49% green leaves) 3 (50% of the canopy is green), 4 (50-90% green canopy) and 5 (in full leaf). We used the mean green up scores for every collection period to track the *C. mopane* population leaf drop through the dry season and as a basis to compare leaf drop with leaf carbon levels.

Environmental data

Meteorological measurements included measurements of net photosynthetically active radiation (PAR, Wm^{-2}). Daily wind speed and temperatures were determined from a weather station deployed 500m away from the site. Data were recorded in hourly intervals. We deployed TDR probes (Campbell Scientific CS615, cm^3 water cm^3 soil) in profiles with 3 measurement depths: at 2cm, 10cm and at ~ 90 cm just above the bedrock. Soil moisture data were logged at 30 minute intervals.

One tree in each treatment was fitted with a Campbell Scientific Infrared thermometer (IRT) which recorded leaf temperature and ambient canopy temperature. This information was logged on an hourly basis.

Leaf carbon gain model

We developed a simple leaf carbon balance model to estimate the daily leaf net carbon balance. We calculated the number of hours leaf stomata were either open or closed across every 24 hour period. We calculated an approximate value of carbon gain when the stomata were open based on leaf photosynthesis measurements which were taken every two hours across a day, across the dry season (see *Tree response measurements*). When the leaves were closed we assumed a baseline value of respiration determined from the light response curves. To achieve this, we first calculated the number of hours each day a plant was transpiring (i.e. open stomata) by comparing actual measured leaf temperature (T_a: measured hourly with the IRT) with the potential leaf temperature (T_p). T_p is the leaf temperature if the stomata were closed and the leaf was not transpiring. This value was determined using the Gates energy balance equation (Norman, 1998) making T_p the subject of the equation.(Appendix B)

To determine if the leaf in the experiment was photosynthesising we compared the T_p if the stomata were closed to the measured leaf temperature T_a as measured by the IRT;

$$T_p - T_a = T_{\text{leaf difference}} \qquad (1)$$

If $T_{\text{leaf difference}}$ was negative, the measured T_a was equal to or higher than T_p therefore the stomata were considered closed and the leaf was not photosynthesising. If the $T_{\text{leaf difference}}$

was positive, it was assumed that the leaf was actively cooling and the stomata were considered open and the leaf was photosynthesising (Figure 1a). Using this method we could calculate the number of hours every day that the stomata were open. Therefore for every hour of the experiment, the representative leaf in each treatment tree could be assigned a value of 1 if the plant stomata were open or 0 indicating the stomata were closed (Figure 1b).

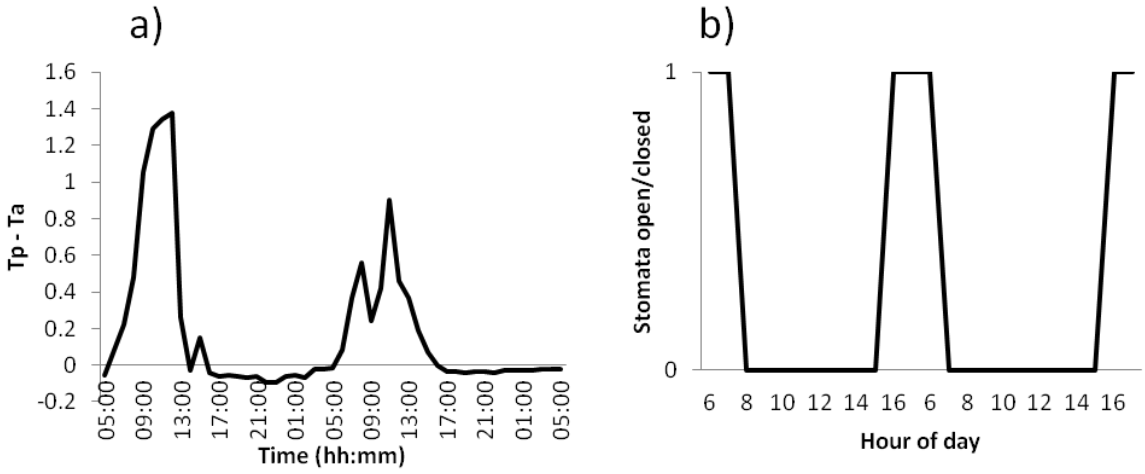

Figure 17a): Example 24 hour period of T_p-T_a. Positive values indicate the stomata are open, negative values indicate they are closed. The calculation indicates that plant stomata are closed at night. B): Example of the diurnal pattern of stomata opening patterns for watered plants. If the value of $T_{\text{leaf difference}}$ was positive it was assigned a 1, if negative, 0.

When the stomata were open, we assumed the plant was photosynthesizing and then calculated a net carbon assimilation rate for that hour of day and day based on the field data collected with the Li-6400 diurnally (8:00, 10:00, 12:00, 2:00, 4:00) and through the dry season (3 May, 2June, 1 July, 12 August) . We assumed a linear change in net-assimilation rates between hourly periods (e.g. between 8am – 10am) and between time periods (i.e. May to June, June to July) and interpolated the data to fill the gaps, thereby obtaining estimates of net assimilation for every hour throughout the study period.

When the stomata were closed we assumed the plant was experiencing a net-carbon loss (Scheiter and Higgins 2009). We assumed a baseline loss value (or respiration value) based on the dark gas exchange measurement (Rdark) obtained from the light response curves that were measured with the Li-6400 during every field campaign. We assumed that respiration remains approximately constant over the day as we did not have more detailed measurements of respiration. As with the values for carbon gain, we interpolated between monthly Rdark

data points assuming linear patterns. The hourly carbon gain or loss was summed for every day, thereby allowing us to calculate an approximate value of net daily carbon gain/loss for each leaf over the duration of the experiment. The net carbon values were converted to g/carbon per day.

Results

Tree response to watering

Watering increased the volumetric soil moisture in the surface and subsurface (>10cm) layers (Figure 2). In the control treatment, the soil water content declined to near zero water throughout the dry season. The elevated soil moisture in the watered treatment decreased the water stress experienced by the trees, as shown by less negative leaf water potential measurements (Figure 3). The leaf water potential of the watered trees did not significantly change as the dry season progressed (ANOVA $F= 0.4398$, $p=0.66$). The non-watered trees experienced a significant decrease in leaf water potential over time (Figure 4), $F_{(2,20)} = 113.4$, $p<0.001$. A post hoc Tukey test confirmed that the leaf water potentials significantly decreased every month.

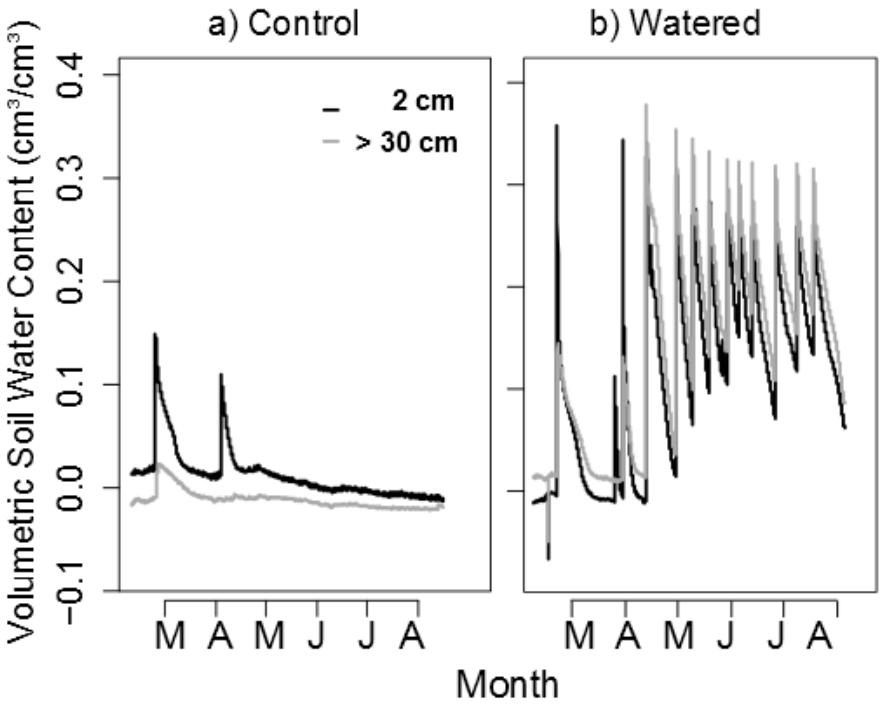

Figure 18: Volumetric soil moisture content for the soil moisture profile of a) control and b) watered trees for shallow (2cm) and 30cm soil depth.

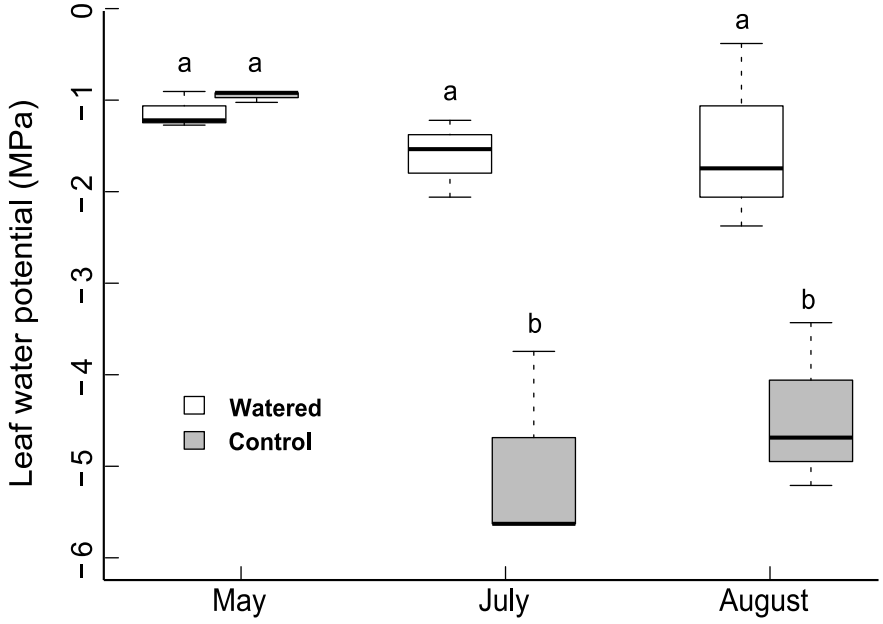

Figure 19: Predawn leaf water potential over time. The leaf water potential of watered trees remained constant over time (F= 0.4398, p=0.66). Control trees became increasingly water stressed ($F_{(2, 20)}$ = 113.4 $p < 0.001$).

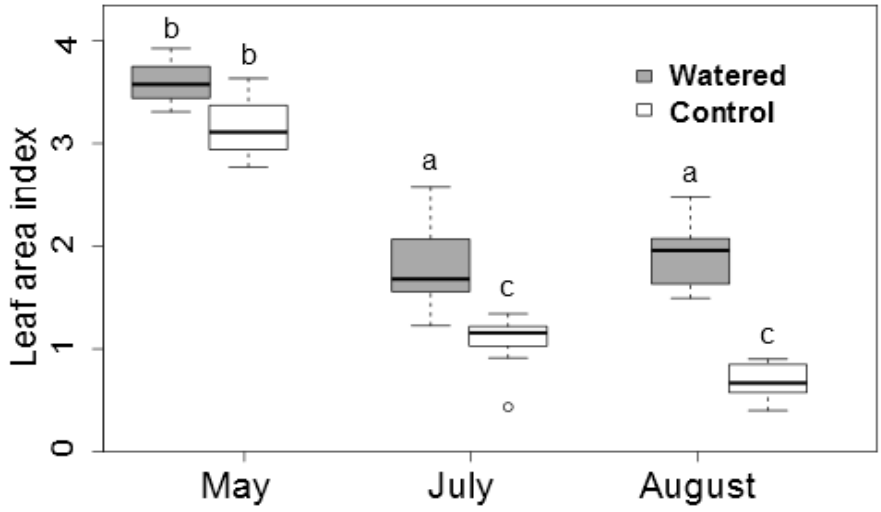

Figure 20: Leaf area index of watered and control trees. Watered trees lost significantly fewer leaves than control trees ($F_{1, 41}$=88.088, p<0.05).The number of leaves on watered trees declined initially during the dry season, presumably as watering covered only the base of the trees and not the entire root extent. Leaf loss stabilized over the season. Leaves in the control trees were lost over time, until August when the canopy was leafless ($F_{2,41}$= 4.932, p<0.012).

Water availability reduces leaf drop; control trees gradually lost all their leaves over the season, whereas the watered trees retained more than half of their canopy (Figure 4). The watering occurred around the base of the tree, and certainly did not cover the full extent of the root system (estimated at 3-5 times the canopy of the tree for mopane (AM Swemmer *pers comm*.), so presumably in the watered trees leaves were dropped until there was enough water to support the remaining leaves. The watered and control leaves also did not age in the same way. In the absence of added water, leaf health declined to almost non-functional states at the end of the season (Figure 6) whereas watered trees maintained ~60% of their leaves in a healthy green state (Figure 5, 6). This had implications for patterns of leaf display in the following season. In the control, all the old leaves were lost at the end of the dry season and were replaced at the beginning of the wet season by new healthy 100% green leaves, representing category 1 and 2 leaves (Figure 5). In the watered trees 60% of the leaves remaining at the end of the season were still 95% or more green (category 1, 2, 3). This influenced the number of new leaves that were initiated and, by January, 40% of the leaves in the watered treatment were still being carried over from the previous year. As demonstrated

from the fluorometry (Figure 6), the leaves in these categories remained healthy and photosynthesised actively (Figure 7).

C. mopane trees photosynthesized throughout the dry season (Figure 7), however, photosynthetic rates did decline in both treatments until the coldest month (July) after which they increased again. Leaves on watered trees always photosynthesized at a significantly higher rate than their non-watered controls and because, unlike the control trees, they did not lose their leaves in August, their photosynthetic rates were back to pre-winter levels by November (after the first rains in October), in spite of the age of the leaves (one year old). The photosynthetic rates of the new leaves on the control trees only equaled the rates of the previous season's watered leaves in January, a full 2 months after leaf burst.

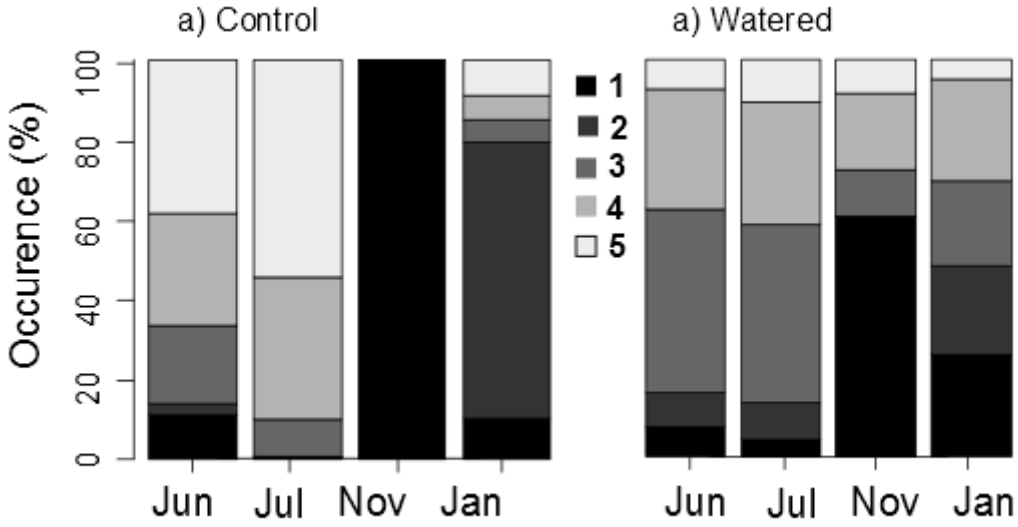

Figure 21a: Leaf health index for a) control and (b) watered trees. Leaf index reflects the leaf health based on the colour and age. Index 1) leaf was 100% green and not fully grown, 2) Leaf was fully expanded and 100% green, 3) leaf was healthy and 95% green but had small black spots, 4) leaf was less than 60% brown 5) leaf was more than 60% brown.

Figure 5b: Leaf health of a) control tree and b) watered tree in the early July field campaign.

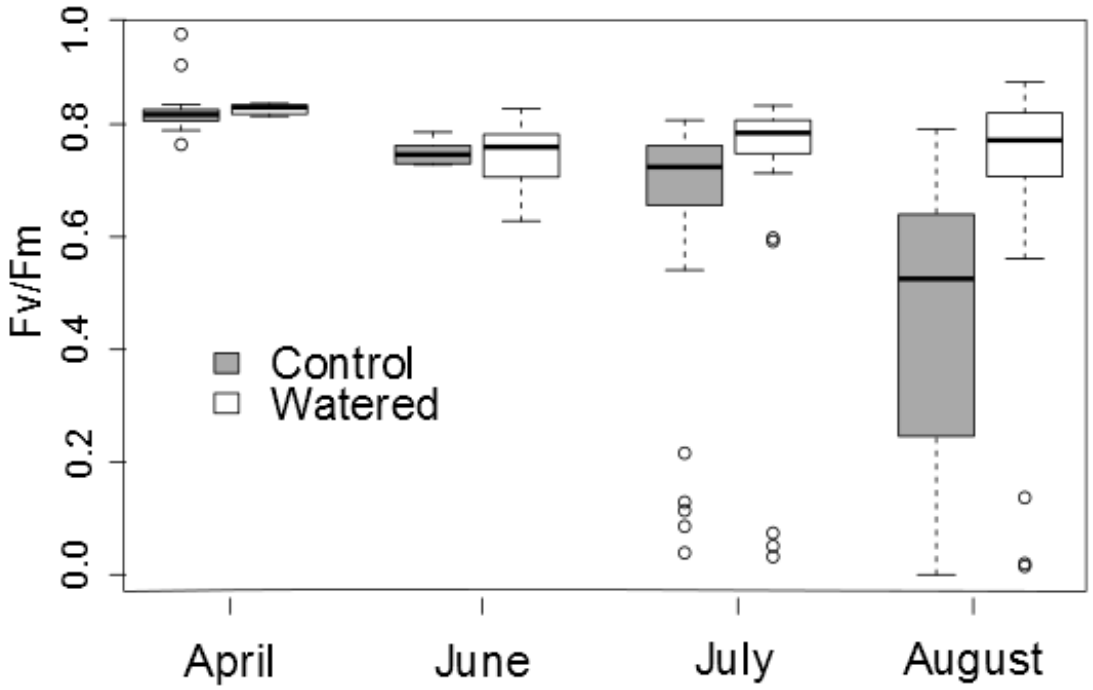

Figure 22: Leaf fluorescence results for watered (grey) and control (white) leaves across months during the dry season. Although the canopy was largely leafless in August measurements were taken on the few remaining leaves. Leaf health of control leaves declined at the end of the dry season.

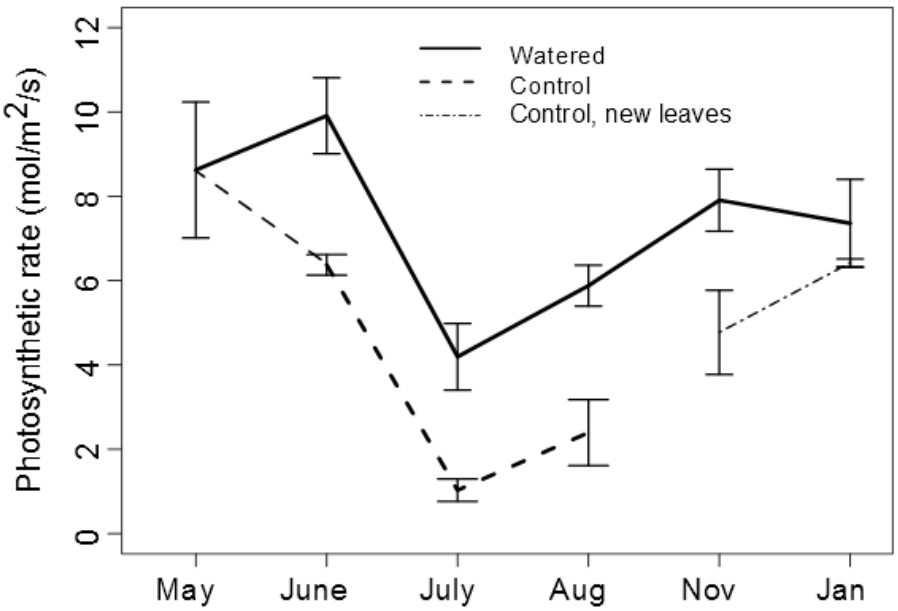

Figure 23: Mean leaf photosynthesis at 10am of watered and control trees across the experimental period. Bars indicate standard errors. First set of readings were taken prior to watering.

Leaf carbon gain

We plotted the daily leaf carbon gain for the watered and control trees for the duration of the experiment and compared the daily carbon gain for dry trees to the average leaf phenology of *C. mopane* measured over the landscape (Fig 8). Daily leaf carbon gain was highest for the watered trees and the leaf carbon gain never declined to zero. Using hierarchical partitioning, we demonstrated that in the control plants, the decline of soil moisture explained 69% of the reduction in leaf carbon gain, whilst 25% was explained by mean daily temperatures. When water was available, mean daily temperature explained 81 % of the change in leaf carbon. Net solar radiation and mean daily vapour pressure deficit explained 10.7% and 7.2% of the leaf carbon gain respectively. Thus declining soil moisture, and to a lesser extent cool temperatures drove declines in leaf carbon gain. Leaf drop was not initiated when photosynthesis reached a zero C balance. Leaf drop in the control trees started when leaf carbon was still positive at ~1.6 g C/day/m^2. When these leaf carbon levels were reached in the irrigated plants, leaf drop did not significantly change strongly indicating that a leaf C threshold is not driving leaf drop.

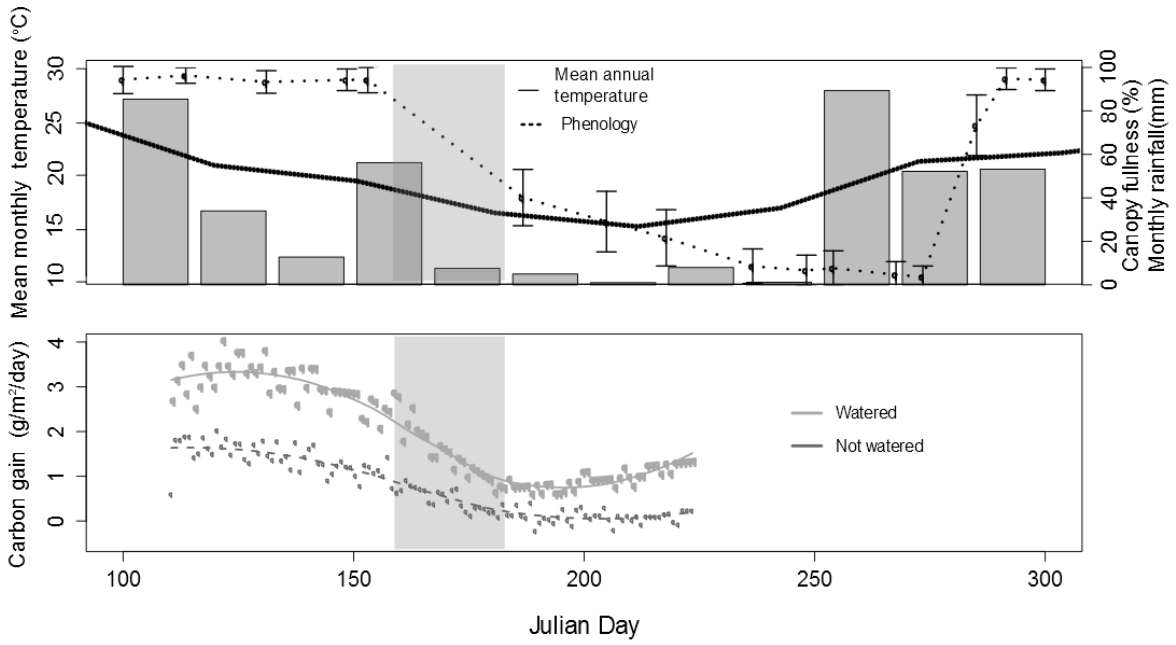

Figure 24: Top graph represents the cumulative monthly rainfall (bar graphs), mean monthly temperature (solid line) and the mean community phenology of *C. mopane* at the landscape level (dashed line). Bars indicate standard errors. The lower graph represents modelled daily carbon gain per unit m^2 of leaf, for the watered (grey) and control (black) leaves for the experimental period. Shaded grey areas on both graphs indicate the period of maximum leaf fall.

Discussion

In contrast to results from tropical dry forests, our results indicate that soil water availability is a primary cue for leaf drop in a dominant tree species in dry African savannas. Deciduousity in *C.mopane* was facultative, with plants retaining their leaves and actively photosynthesising when water was supplied in the dry season. This further indicates that in this species leaf age is not an important factor driving leaf drop.

Leaf drop cues

In savannas where a distinct dry season occurs, water stress is an obvious candidate as the primary cue for leaf drop (Borchert 1994; Wright & Cornejo 1990) and is often used to drive phenology in DGVM models (e.g. Stitch et al. 2008). Our results for the arid-adapted *C. mopane* support this hypothesis. This is in contrast to results from irrigation studies performed in tropical forests where many trees tend towards obligate deciduousness (Wright & Cornejo 1990; Reich 1994). We could find only one study in a dry system where watering completely prevented leaf loss throughout the entire dry season; 83% of *Toona ciliate,* a

tropical Australian forest tree, retained their leaves throughout the dry season when watered (Heinrich & Banks 2006). Overall the most common responses to irrigation is earlier leaf flushing the following growing season (Myers et al. 1998; Wright & Cornejo 1990) or delayed leaf fall (Myers 1998; Wright & Cornejo 1990; Lobo et al. 2008). Most species in previous studies showed no response to watering, and leaf longevity remained unchanged. Whether the contrasting results shown here for *C .mopane* apply to the other dominant woody species of African savannas remains to be determined; however, as *C. mopane* dominates a third of southern African savannas the information we have gathered is highly relevant. Our results are consistent with some field observations of other savanna species. For example, Shackelton (1999) found in a South African savanna region that leaf fall occurred later a mesic site relative to an arid site, and that within a site, leaf fall occurred early on uplands relative to bottomlands (the former having lower soil water capacity and presumably drying down faster as the dry season progresses).

C. mopane is exceptional in that it retains its leaves long into the dry season relative other co-occuring savanna species (Dekker & Smit1996; *pers. obs.*). It may therefore not be responding to the same environmental cues, or it may simply have a different threshold for leaf drop on the same cues. The slowness to shed leaves may be an adaptation to exploit low levels of soil moisture during frequent summer droughts, or to take advantage of rainfall events that do occasionally occur in the dry season. It is possible that other savanna species have evolved different strategies to cope with aridity, including obligate deciduousity in some cases. Development of the theory regarding obligate deciduousity, beyond the well established controls of temperature and day length relevant to temperate zones, is needed for arid and semi-arid savanna zones.

Leaf carbon balance

Leaf drop in *C. mopane* was not determined by leaf age, or by our modeled estimates of leaf carbon balance, contrary to the leaf optimal carbon gain hypothesis (Kikuzawa 1994; Vincent 2006; Reich et al. 2009). Leaf drop in the control *C. mopane* trees occurred when leaf carbon values were still positive and the leaves were still photosynthesizing, albeit at very low rates (Fig. 7 & 8). When comparable leaf carbon values were met in the watered trees, overall leaf drop did not occur. Thus carbon balance at the individual leaf level does not drive leaf drop. However, as we did not measure whole plant respiration costs we cannot determine if leaves were dropped at a threshold based on whole plant net carbon (Givnish 2002). A plausible

alternative is that declining water availability was the direct cause of leaf drop. Leaf loss can occur to prevent additional reduction in the water status of the plant through transpiration, even though the leaves are still photosynthesizing.

Leaf aging, especially in deciduous species is stated to decrease photosynthesis and increase the likelihood of leaf senescence (Acklerly & Bazzaz 1995; Kitajima et al. 1997; Borchert et al. 2002). The leaves of *C. mopane* demonstrated no such relationship, as when they exceeded a year in age, photosynthetic rates in the watered (1 year old) leaves continued to photosynthesise at pre-dry season levels in the subsequent wet season. Similar responses of non-age related seasonal declines in assimilation have been noted in a mesic savanna by Prior et al. (1997) for a *Eucalyptus* species. Our results suggest that climatic effects are more important in driving leaf carbon levels than leaf age. Water availability, temperature and solar radiation all contributed to declining leaf carbon uptake in the dry season.

Our results indicate that even un-watered *C. mopane* gain carbon well into the dry season. The advantage of this attribute in an ecosystem where carbon is not generally limiting is unknown. It may be an inadvertent by-product of being extremely tolerant of mid- wet season droughts, i.e. *C. mopane* leaves are adapted to endure a period of month or so of low water availability, before senescing, as such periods often occur during the growing season, and maintaining leaves through them would be more efficient (for carbon and nutrient retention) than replacing a full canopy of leaves. Alternatively, as *C. mopane* is such an aggressive resprouter (Timberlake 1992; Kohi et al. 2010), the extra carbon gained as a result of an extended growing season could be used for carbohydrate storage in roots, allowing for stronger resprouting following severe above-ground damage from elephants, fire or Mopane worms (*Gonimbrasia belina*). A third possibility is that the prolonged leaf display by *C. mopane* disadvantages potential competitors. By maintaining a canopy of actively photosynthesizing leaves, *C. mopane* trees can draw down soil moisture to lower levels than would occur if all their leaves had dropped. As *C. mopane* is shallow rooted (Timberlake 1995; Smit et al. 1998) this could create conditions that are too dry for competing plants (woody or herbaceous) to endure, or could slow the growth of competing plants at the start of the subsequent growing season, as soil water levels would have to increase from a lower base before growth can begin. A similar idea has been proposed by Ward et al. (2013) who propose that their abundant shallow roots and higher water-use efficiency allow *C. mopane* to outcompete co-occurring grasses.

Facultative deciduousness and future distributions

The benefit of facultative deciduousness to *C. mopane* in response to global climate change will depend on how seasonality of rainfall changes in southern Africa. Increased rainfall, particularly at the end of the growing season or during the dry season, may benefit *C. mopane* through increasing the duration available for carbon acquisition. If it results in functional, mature leaves being retained throughout the dry season, that would allow *C. mopane* to photosynthesis at near-maximum rates immediately at the start of the subsequent growing season, when critical resources (such as nitrogen) are abundant (Scholes & Walker 1993). Non-facultative species would still suffer a development lag before peak photosynthesis is reached (which, from our data, could be as long as two months). Additionally, the ability to maintain leaves for more than one growing season would prevent a mass loss of nitrogen, and allow for nutrient losses to be reduced and spread out over time. Warmer temperatures might increase such benefits for facultatively deciduous species, allowing for greater rates of photosynthesis during the dry season.

Conclusions

Water stress is the critical cue driving leaf loss of *C. mopane*, and had a strong effect on leaf carbon levels. While our experimental results cannot precisely identify which mechanism drives leaf loss, we can conclude that leaf loss is facultative and does not occur through leaf aging. Leaf loss is also not based on individual leaf carbon balance becoming negative or crossing a particular C balance threshold. Although *C. mopane*, grows in seasonal, arid savannas, it retains leaves late into the dry season and remains photosynthetically active while leaves are present. This atypical response may hold some clues as to its dominance in this environment. It also raises some questions, regarding the costs and benefits of facultative decidiousity. The behavior of this species indicates that obligate deciduosity is not the only successful strategy in climates with a long dry season.

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Chapter 7: Conclusions

Thesis summary

In this thesis I set out to assess how global change can influence South African savannas. I considered two scales; that of the entire woody layer across wider climate gradients, and that of individual species in a case study. At the regional scale I examined tree cover change across different land uses, and for individual species I investigated what might limit their distribution at each critical demographic stage. Both approaches have proved informative and have led to new insights.

Tree cover changes

I have documented widespread tree cover increases in South African savannas across four distinct land uses. It is one of the few investigations recording tree cover change at a regional scale over several decades (70 years). Previously the largest scale study in South Africa, over a similar time period, covered an area of 75km^2 (Wigley et al, 2010). In this study I measure change over almost 1000km^2. The study provides compelling evidence that a global driver, and not only land-use, is a major contributor to tree cover increase across South African savannas. Rainfall decreases, not increases, were documented for a large portion of the study area, and were therefore rejected as the primary cause of tree cover increases (Kruger, 2006). However, as measured changes in rainfall are not available for every individual site, I cannot completely exclude the possibility that some cover increases are driven by rainfall increases (Kulmatiski & Beard, 2013; Russell & Ward, 2014). Elevated CO_2 was the most likely cause of tree cover increases, and the results were consistent with existing studies on CO_2 effects. Whilst elevated CO_2 is likely to be the primary cause of the observed changes, I also demonstrated that elephants prevent tree cover increases, but only in the arid and semi-arid savannas. This indicates that the widespread extirpation of the megafauna in savannas has had a regional impact on savanna structure and function. The loss of complete suites of herbivores should therefore be considered as a a) regional scale change with regional consequences b) a potential additional cause in widespread tree cover increases in arid and semi-arid savannas. This study also showed woody thickening is occurring in the arid and semi-arid stable savannas. Whilst thickening has been documented in small scale studies across Africa, most studies that implicate elevated CO_2 as a cause have only produced evidence of increases in mesic savannas (Wigley et al, 2010; Buitenwerf et al, 2012; for

review see Bond & Midgley, 2012). Therefore this is one of the few studies in Africa that demonstrates arid and semi-arid savannas are also experiencing woody cover increases similar to that of mesic savannas (but see Donohue et al, 2013; Mitchard & Flintrop, 2013)

Understanding the distribution limits of savanna trees

Secondly I considered how savanna tree distribution might be altered with climate change. Here the challenge lies in first understanding what causes existing distribution limits. Using a correlative species distribution model, I set out to identify key climatic variables that might limit the distribution of *Colophospermum mopane*, an important arid savanna dominant in southern Africa (Chapter 3). The species distribution model demonstrated that climatic variables, particularly cold season temperatures, rainfall and dry season day length (which can be interpreted as a measure of latitude) were important predictors of the distribution limit of *C. mopane.*

However, experimental studies of different climate factors at successive demographic stages failed to support the correlative models in that no strong climate controls on distribution were identified. At the seedling stage, growing season temperatures did not directly limit the germination of the study species (Chapter 4). Germination events would be frequent under current and warmer climates. Successful early seedling establishment is, however, limited by water availability and is pulsed. An increase in temperatures will promote seedling growth rates and is likely to improve seedling establishment probabilities. A large transplant experiment (over 8 degrees of latitude) showed that young saplings were able to grow 100s of km's south of their current distribution limits (Chapter 5) so that climate did not explain the distribution limits of either species. A combination of grass competition and fire return intervals determined the probability of sapling escape from the fire trap. Escape probability was a good predictor of the distribution of the study species. Both *C. mopane* and *A. nigrescens* can be characterised by different escape probabilities, which also explains differences in their distribution ranges. At the adult stage (Chapter 6) I demonstrated that if sufficient water is available *C. mopane* leaves are facultatively deciduous and plants can photosynthesise at higher rates, and gain more carbon late into the dry season. However *C. mopane* range stops as rainfall increases, suggesting that additional water availability at the adult stage will not release the plants from their current range limitation. Warmer temperatures however have the potential to increase photosynthetic rates in the dry season if water is present in the system.

The analysis of determinants of the distribution limits of *C. mopane* and, to a lesser extent, *A. nigrescens* show the determinants of ranges in these tropical savanna species are complex, and multiple factors interact to affect the performance and success of these species at different demographic stages. As climate does not definitively limit the distribution limits of these plants, we did not demonstrate a "hard limit" to plant ranges. It is therefore likely that the formation of range limits is a sequential process, where a numerical decline of individuals cumulates through each demographic stage. I suggest that, as savannas are heterogeneous systems, and in the absence of a "hard climatic limitation", the presence of a plant is dependent on biotic (competition) and consumer controls (fire and herbivory), thus there remains a chance that individuals will escape their limitation at each demographic stage. To account for the distribution range of a species, multiple limitations probably occur at key demographic stages (some stronger than others). I highlight three factors which are likely be strong filters in setting distribution limits

a) At the seedling stage the high germination sensitivity of *C. mopane* seeds may cause a potential seed stock limitation as the frequency of germination events, not necessarily the frequency of suitable establishment conditions, increases with increasing rainfall.
b) At the sapling stage a combination of higher grass productivity and frequent fire return intervals are important in determining the escape of these trees from the fire trap. High grass biomass and a high fire frequency, driven by a higher rainfall will prevent slow-growing saplings from successfully transitioning to adult trees.
c) Frost will reduce sapling growth rates and ultimately prevent escape from the fire trap. Successful establishment in natural conditions (where fire and herbivory occur) is unlikely in areas which are frosted frequently.

These new insights allow further exploration into the question of how savanna trees could respond to a warmer world. The study species are well adapted to survive and grow under hot, arid conditions, to the extent that warmer temperatures can even be an advantage these species. Therefore, as opposed to general predictions that range shifts (pole wards or upwards) will occur in response to warmer conditions, these species may benefit and experience range extensions (as opposed to range shifts). Current predictions for precipitation trends in the low elevation savannas are poorly defined for South Africa (e.g. DEA, (2011; 2013) with some models suggesting that rainfall will remain stable or increase by less than

10% (Engelbrecht et al, 2013). Changes in rainfall, may change the performance of my study species, however both species are well adapted to dry conditions and unless the changes are huge it is unlikely that this will cause any catastrophic changes in the population.

The experimental studies reported here demonstrate that, within realistic climate bounds, climate does not directly limit the distribution of these savanna trees. This has implications for predicting climate change responses of savanna trees. The predictive frameworks which assume plant distribution is set by climate, e.g. correlative species distribution models, are not appropriate methods for predicting change in savannas. It can be argued that species distribution models, even if they do not imply causality, are useful to highlight areas vulnerable to change (DEA, 2013), however I argue that knowledge of the underlying mechanisms prevents incorrect assumptions from being made. Rather, when predicting changes, we should explicitly consider how changing land-use and consumer controls (i.e. fire and herbivory) will affect species ranges. The dominant land use practices in savannas all variously alter factors that can affect species distributions e.g. grass biomass, fire and the type of herbivory, and thus should be explicit in future predictions. As consumer controls, especially the fire regime, can influence the distribution of savanna species we should also consider how climate changes interact with consumer controls like fire regimes and herbivore distribution.

The combination of the findings in this thesis makes a novel contribution to science and savanna ecology by providing a new framework from which to consider global change in savannas.

Where to from here?

An alternative framework of savanna species distribution

This thesis highlights that climate is not a useful predictor of changes in savanna tree distribution and indicates that consumer controls need to be considered. This hypothesis is relevant as distribution of the savanna biome itself is not uniquely predictable from climate - grasslands, tropical forests, savannas can all occur within the same climate space (Whittaker, 1975; Bond, 2005; Bond et al, 2005; Lehman et al, 2011; Hirota et al. 2011; Staver et al. 2011). The distribution and structure of savannas is often set by consumer control, i.e. fire and herbivory, which prevent vegetation biomass from reaching its climate potential (Bond & Keeley, 2005). Here, fire and herbivory do not simply act as disturbances, but have

influenced the evolution of plants and their traits over millions of years ((e.g. for fire see Pausas & Keeley, 2008; Bowman et al, 2009; for defences against mammalian herbivory see Stebbins, 1981; Mack & Thompson, 1982; Coughenour, 1985; Owen-Smith, 1988). Therefore it is also reasonable to propose that consumer controls will influence savanna tree distributions.

I therefore propose that within a savanna context the action of fire and herbivory set environmental filters, equivalent to that of climatic factors in temperate systems. If this were the case, then, by understanding the distribution and dominance of fire and herbivory filters across a savanna rainfall gradient, we should be able to predict the distribution of many savanna tree species at both regional and local scales. To establish a framework from which to investigate savanna tree range limits, I used clues from several continental scale analyses of savannas to determine the most probable environmental filters, including consumers, across a precipitation gradient (Sankaran et al 2005; Archibald 2009, Lehmann et al 2011) (Figure 2).

At the arid end of savannas (~300 -450mm), fire and herbivory levels are low and tree cover is strongly limited by water availability (Sankaran et al, 2005; Archibald et al, 2009). Here the critically limiting demographic stage is the seedling establishment stage (Harrington, 1991; Higgins et al, 2000; Kraaij & Ward, 2006, Chapter 4); where seedling establishment is limited by water availability. For seedlings to survive this transition they need to have evolved traits to survive low, infrequent and unpredictable rain events in the growing season such as rapid germination and radicle extension when conditions are suitable (Chapter 4).

As rainfall increases mammalian herbivore biomass and herbivory levels increase, reaching their peak in semi-arid savannas (500 – 700mm) (Hempson et al in review), while fires are most frequent in more humid savannas (850 – 1400mm) (Archibald et al. 2009; Lehmann et al, 2011).Trees growing in these moister semi-arid and mesic savannas experience a population bottleneck at the sapling stage and sapling transitions to larger tree sizes require periodic escape from a browse or fire trap (Hoffman, 1999; Higgins et al, 2000; Prior et al, 2010). For saplings to survive this transition they need to have evolved traits to survive either fire or herbivory e.g. a cagey sapling architecture to reduce biomass loss to herbivory (Archibald & Bond, 2003; Staver et al, 2012; Dantas & Pausas, 2013). However, an important missing component of this framework is an understanding of how grass

competition interacts with initial seedling establishment and subsequent seedling survival across the rainfall gradient.

Each driver (rainfall, fire and herbivory) is the dominant filter across different areas of the rainfall gradient (Figure 1). Where each driver is dominant, it should act as a strong filter for species occurrence, and only species with specific traits that enable success in the presence of the dominant filter, especially at the critically limiting demographic stage, will occur in that area. For example, a plant with fire adapted sapling traits (e.g. pole like architecture) will be able to successfully establish in an area with regular fires but is less likely to overcome the seedling establishment bottleneck in arid savannas. I do not suggest that all traits of plant will be geared to only surviving the dominant filter as environmental filters overlap and plants need to cope with impacts from filters common across the rainfall gradient e.g. insect herbivory. Nevertheless, I suggest that the critical demographic bottleneck will vary across a precipitation gradient because of predicable changes in the importance of key environmental filters.

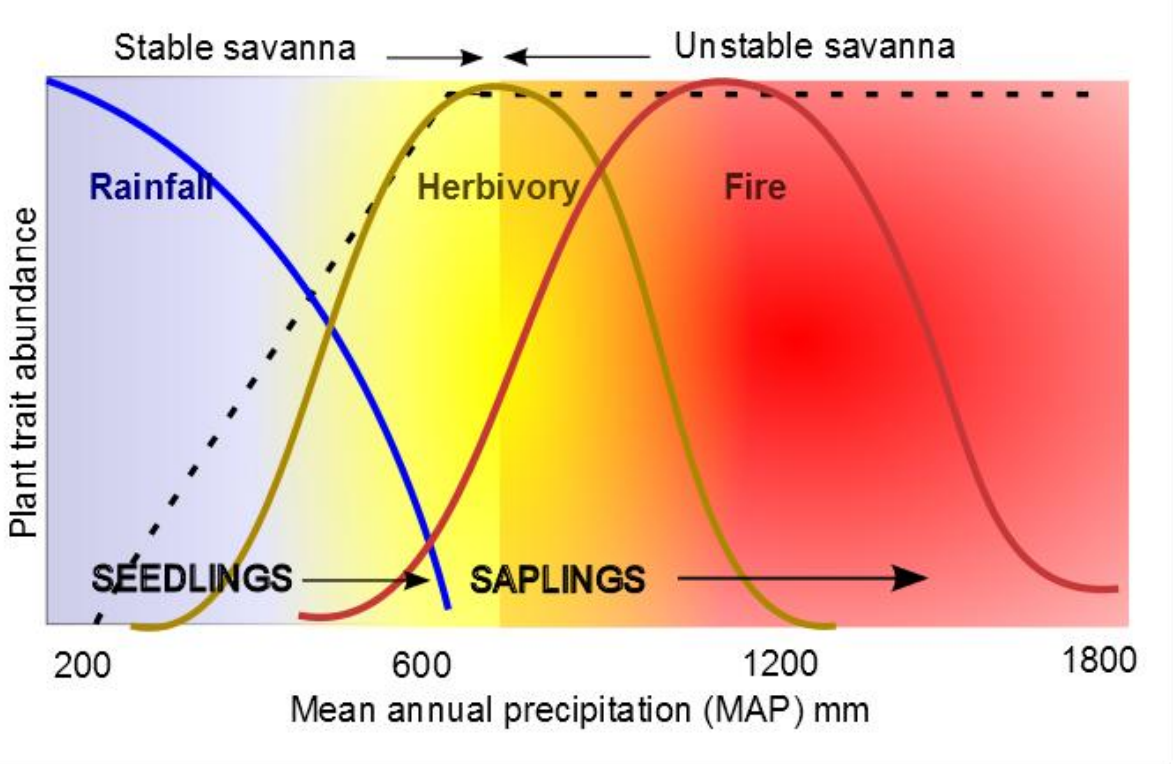

Figure 1: The distribution of the dominant drivers across a rainfall gradient according to a conceptual framework for key environmental filters influencing woody species distribution in African savannas. The life-history stage at which the dominant driver is the strongest filter to plant success will possess

filter-specific traits. Hence consumer controls are also critical in shaping species distributions in savannas.

This framework provides a potential alternative to climate based species distribution models. The predictive ability of this model will not be as clear as climatic framework as consumer controls are unlikely to set "hard" distribution limits and; a) fire and herbivory are readily manipulated in space and time and are subject to positive feedbacks b) there is overlap of these filters across the rainfall gradient and, c) biotically created heterogeneity can extend or change the dominant filters at local scales e.g. the presence of termite mounds in a fire dominated savanna will allow fire sensitive species to occur in the area (Plas et al, 2013).This may produce a situation where, in contrast to a climatically defined niche space where biotic interactions reduce the range of a species, biotic interactions and local heterogeneity increase the range of plants.

This framework provides an alternative way to understand current species distributions in savannas and offers, where species distributions are consumer controlled, opportunities for managing changing distributions by appropriate interventions in fire and mammal management

Future work: Developing and testing an alternative framework of savanna tree distribution.

To test this hypothesis we need to establish the distribution of plant traits, at the relevant critical demographic stage, across the rainfall gradient (according to Figure 1). We need to focus future work on the following:

1. Test across species, across the rainfall gradient, where the critical population demographic bottleneck occurs.
2. As two main bottlenecks occur, at the seedling establishment and sapling stage, relevant traits to record include those influencing
    a. Seedling establishment: a) Seed dormancy (presence and type) , b) germination speed c) radicle extension rates
    b. Saplings a) Tree architecture (cage vs. pole) b) maximum growth rate c) resprouting response.
3. Determine whether plant traits correspond with predicted dominant filters across a rainfall and soil nutrient gradient at each critical demographic stage

a. At local scales: Does species composition and species traits match predictions in areas where fire, not mammalian herbivory has been excluded and vice versa
b. Regional scales: Does the frequency of traits fit predictions on the hypothesised dominant filter at the limiting demographic stage?

Evolution of the PhD: An informal perspective

This PhD was developed to broadly understand how savannas will respond to global change. The earliest ideas and questions were formulated based on ideas dominant in the literature that climate and elevated CO_2 were going to produce large changes in savanna structure and function. I therefore approached this study, especially the tree distribution case study, with the underlying assumption that the savanna tree ranges were climatically limited. I predicted that a demographic specific view would reveal a clear "hard" limit of species ranges at one demographic stage. The range of results, especially from the transplant experiment, highlighted the deficiencies and oversimplification of the initial framework.

Climate, especially water availability, was important, but was not clearly limiting these plants. The biggest switch in my perspective arose from site visits where I could observe that a) in spite of variable climates species were surviving and growing quite well everywhere and b) tree success was strongly affected by grass. This field experience revealed the need for considering alternative avenues to exploring drivers of distribution limits.

Overall this study has revealed to me the importance of understanding the context in which a plant grows. It also highlights, quite shockingly, how much tree cover has increased within savannas. The biodiversity impacts of this increased cover and likely structural homogenisation are negative and large. Climate change will have impacts of savanna structure and function, but we should be focusing on understanding how climate change will affect the drivers of savanna structure and function. While demographic studies on single species studies are not common in savanna ecology in general, they add value to science in a changing worlld. Climate change and elevated CO_2 are raised as potential threats to savanna structure and function, and indeed they are. However land-use change and widespread extirpation of large mammals should also be considered as equally important regional drivers, and potential agents of change.

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Appendix

APPENDIX A.

Detailed description of methods used in Chapter 4

A.1 *Data Analysis*

Thermal time modelling

Thermal time model parameters were calculated from the germination data generated from the TGP. Cumulative germination curves were plotted for each temperature regime and the time (t) taken to reach 50 % of the final proportion of germinated seeds at each temperature was calculated (t_{50}) from these curves. The $1/t_{50}$ was plotted against temperature (using R software version 15.0) to produce a linear relationship where estimates were made of the base temperature (T_b), below which $1/t_{50}$ is equal to zero, the ceiling temperature (T_c), above which $1/t_{50}$ is equal to zero (Covell *et al*., 1986; Ellis *et al*., 1986) and the optimum temperature (T_o), taken as the intercept of the sub- and supra-optimal temperature linear regression lines (Hardegree, 2006). For each species, the thermal time (θ_T) for fraction G of the population to germinate at each sub-optimal temperature was calculated using the equation below:

$$\theta_{T(G)} = (T_G - T_{bG})\, t_G \qquad \text{equation 1.}$$

where T_G is temperature, T_{bG} is base temperature as determined from the repeated probit analysis and t_G time since start of imbibition (Covell *et al*., 1986). A repeated probit analysis (Bradford, 1990) was performed in Genstat (version 11.1.0.1575, VSN International Ltd, UK) on germination values and their corresponding log-thermal time [$\log_{10} (T_g - T_{bg})\, t_g$], varying the value of T_{bG} until the best fit was obtained, using the following equation (Covell *et al*., 1986; Bradford, 1995, Daws *et al*., 2004).

$$\text{probit}\,(_G) = \{\log [(T_G - T_{bG})\, t_G\,] - \log [\theta_T(50)]\}/\sigma_{\theta T} \qquad \text{equation 2.}$$

Where probit ($_G$) is the probit transformation of the cumulative germination ($_G$), $\theta_T(50)$ is the median thermal time to germination and $\sigma_{\theta T}$ is the standard deviation of $\log \theta_T\,(50)$. Data points where germination did not increase for more than three consecutive days were excluded from the analysis.

Hydrotime modelling

Seed germination responses to water potential can be described on a hydrotime scale (Gummerson, 1986). We calculated the hydrotime for each water stress treatment. As with thermal time we calculated the time (t) taken to reach 50 % of the final proportion of germinated seeds at each water potential (t_{50}). We tested for a linear relationship between the $1/t_{(50)}$ and water potential (using R software version 15.0) to obtain estimates of the base water potential (Ψ_b), (Bradford 1995; Gummerson, 1986;). The hydrotime (θ_H) for fraction G of the population to germinate at each water potential temperature was calculated using the equation below:

$$\theta_{H(G)} = (\Psi_G - \Psi_{bG})\, t_G \qquad \text{equation 3.}$$

where Ψ_G is the water potential, Ψ_{bG} is base water potential as determined from the repeated probit analysis and t_G time since start of imbibition (Bradford, 1995; Gummerson, 1986,). A repeated probit analysis was applied where all Ψ_G were regressed against $\Psi_G - (\theta_H / t_G)$, until the best fit was obtained (Bradford, 1990), according to the equation (Eq 4).

$$\text{probit}(g) = [\Psi_G - (\theta_H / t_G) - \Psi_b(50)]/\sigma_{\Psi b} \qquad \text{equation 4.}$$

Where $\Psi_b(50)$ is the median of Ψ_b, and $\sigma_{\Psi b}$ is the standard deviation in Ψ amongst the seeds within the population.

Radicle extension

Unequal germination between treatments resulted in radicle length data with an unbalanced design. Data were analysed using linear-mixed effects models in the nlme package (Pinheiro *et al*., 2009) for R (R Development Core Team 2012). Model selection was performed by constructing a full model in which all fixed predictors and their interactions were present and subsequently removing all non-significant terms. The germination box was initially included as a random variable and as its contribution to the models was extremely small the analysis was performed without random variables using the generalised least squares model. Significance of fixed terms was determined with marginal l F-tests (Pinheiro & Bates, 2000).

A.2 Soil moisture model

Water balance models track the inputs and outputs to the soil column. Here, rainfall was the input and losses occurred through interception, run-off, evaporation, transpiration, and leaching were the outputs. Soil properties controlled infiltration rates and water holding capacity. Vegetation cover (FAPAR) controlled interception losses and transpiration rates, and the amount of bare ground and atmospheric properties controlled evaporation rates. The maximum evaporation rate was defined by the open water potential evaporation rate (E_0) calculated from the Penman-Monteith equation with surface resistance set to zero (following the methodology of Allen 1998). At each daily time step the topsoil lost water to evaporation at E_0 * (1-FAPAR) *Available Soil Moisture. Water can be lost from the topsoil *and* subsoil by transpiration at a combined rate of E_0 * FAPAR, subject to a linear constraint imposed by stomatal closure as the soil moisture drops to wilting point.

This model was validated against soil moisture data recorded at the Skukuza Flux Tower, South Africa. This site is the longest running flux tower in South Africa and is also located in the semi-arid Kruger National Park, on similar soils to Malopeni Flux tower site. The validation gave a Mean Absolute Error (MAE) of 1.13% with a slight (5%) under-estimation of soil moisture by the model. Both the size and the duration of the wetting events were well represented by the model (Figure A1). See Archibald and Scholes (2007) for a full description of this model. Because the hydrotime model requires inputs in Mpa, and the bucket model outputs data as volumetric soil moisture (mm/soil volume) these data were converted to MPa using the Van Genuchten equation (Van Genuchten, 1980).

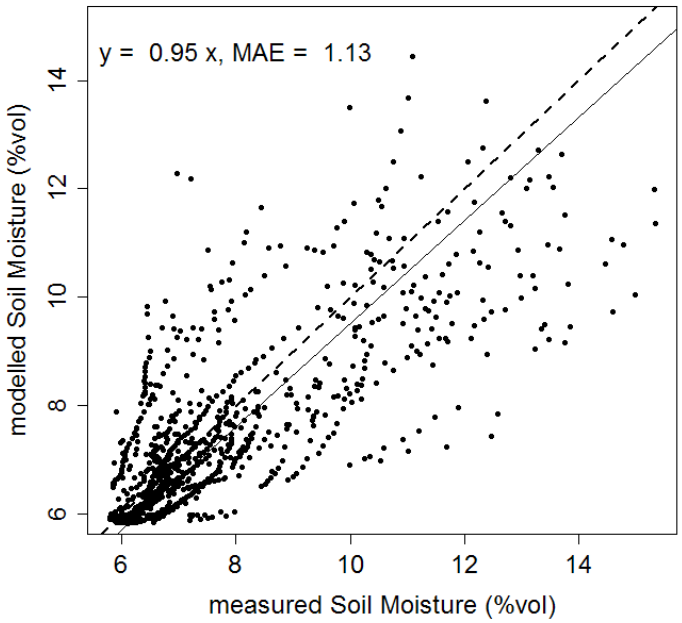

Figure A1: Measured vs. Modelled soil moisture. Dashed line represents a 1:1 relationship; solid line represents the best fit linear model (with an intercept of 0).

A.3 Modeling germination and seedling establishment under field conditions

Air temperature data from the Malopeni site were converted to ground temperatures using a linear conversion developed from two nearby temperature monitoring sites which have thermal loggers at 10 cm above the ground and 1.2 m above the ground (Equation 5: R^2 =0.935).

Ground temperature (°C) = (1.2583 x air temperature (in °C)) – 5.5086

(equation 5)

We started modelling germination events when the first 15ml rainfall event in the rainy season occurred. Each day we calculated θ_T using equation 1 and θ_H using equation 3 and summed the successive daily totals. When both the hydrotime and thermal time requirements were met, we considered this to be a successful germination event – which in the lab was an indication that 50% of the seeds had accumulated sufficient heat and water. However, we assumed that a lower success rate will occur in the field and that each germination event utilised 25% of the total seed stock. Once the soil reached wilting point (< -1.5Mpa), the

counter was reset back to T_0. At wilting point plants are no longer able to take up moisture from the soil and we assumed the same for the seeds. Wilting point can vary from plant to plant but is traditionally set at -1.5 MPa. Although savanna plants almost certainly have a lower wilting point, using a lower value makes little difference to the θ_{WP} since the θ - ψ relationship is very steep in this region of the curve.

For each germination event we then assessed the probability of establishment using lab data on root growth at different water potentials. Roots grew at a rate determined from the radicle extension rates, until the available soil moisture dropped below wilting point, at which point the seedling stopped growing. If the radicle was less than 90mm at this point this was considered a failed establishment event. If the radicle was longer than 90mm by the time the surface soil moisture ran out we considered the establishment event successful, provided there had been <4 germination events (each using an estimated 25% seed stock) in the same wet season. This model was run for three years (2009, 2010 and 2011).

The exact results depend on some of the assumptions of the model, e.g. where we assumed that the seed stock had run out after 4 germination events. We also assumed (based on data from the nearby Malopeni flux tower), that the top ~9cm of the soil was exposed to evaporation. However, the qualitative results should not be impacted by these assumptions, and would hold true for species with the same thermal and hydro germination niches and root extension characteristics

APPENDIX B.

Gates energy balance equation detail

Rnet = Net incoming radiation (w/m^2)	Net incoming radiation measured from net radiometer installed at study site
λ = Latent heat of vaporization of water	44.1 kJ/mol (constant)
Gv = conductance of vapour	= 0.5 * Gvs * Gva / (Gvs + Gva)
Gvs = stomatal conductance (as measured from licor)	
Gva	1.4 * 0.147 *
U= Wind speed (m/s)	Wind speed, measured from anaenometer placed at site
d -= leaf dimension	Average width (0.1) X 0.75 (shape dimension from Campbell book)
D= Vapour pressure defict of the air (kPA)	Calculated from vpd=es∗(100−RH)/100
es = saturation vapour pressure of water at temp T	
RH = relative humidity	Measured from Malopeni flux tower
Ta = Air temp	Measured from thermometer at site
Pa = atmospheric pressure (kPa)	97.7 given the elevation at the site
Cp = specific heat of air at constant pressure	29.3 (table from Campbell 1998)
Ghr= radiative conductance	Temperature dependent constant from (Campbell, 1998) table
s = slope of saturation mole fraction function	
Δ=	153Pa/ C